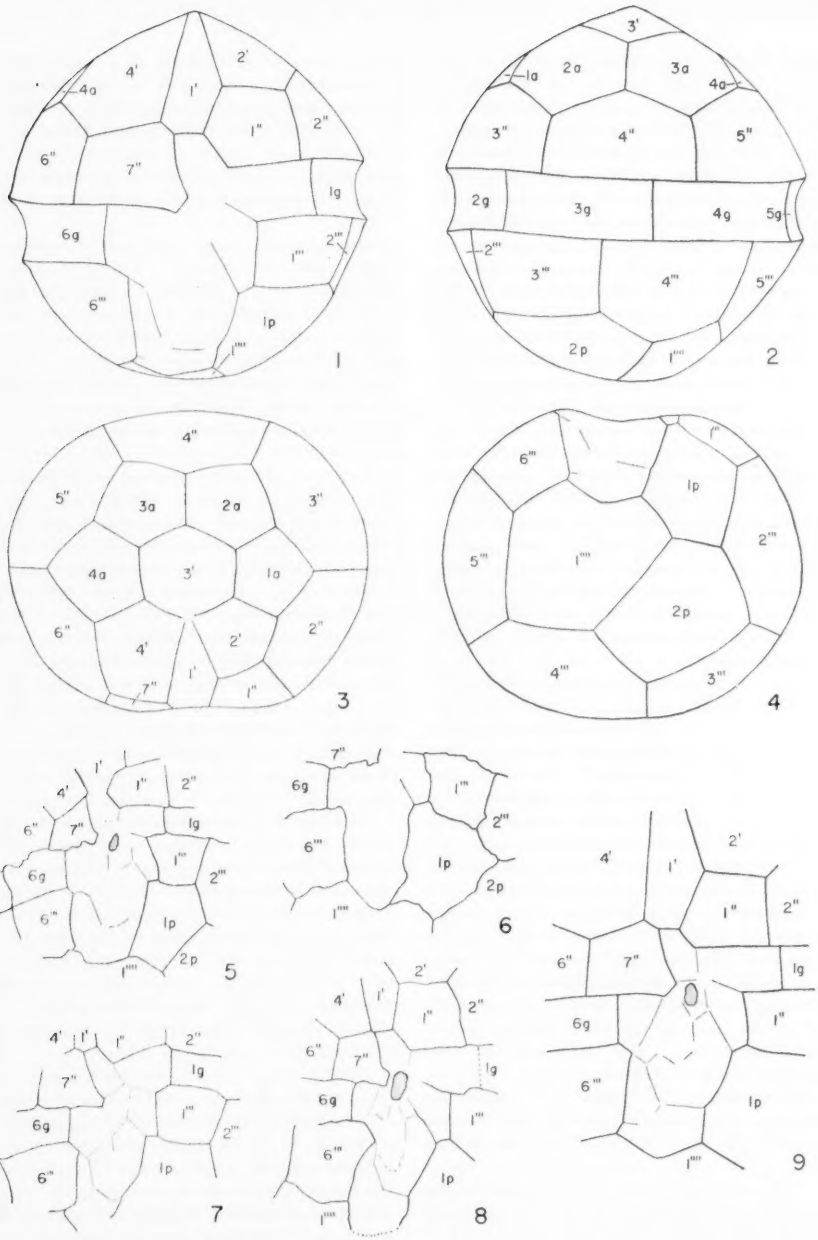



TEXT-FIGS. *1–9*—*Dapcodinium priscum* n. gen., n. sp. *1–4*, diagrams of tabulation in ventral, dorsal, apical and antapical views. *5–8*, camera lucida drawings of ventral areas of four paratypes, ×1500. *5*, #139378; R8.2, +5.8. *6*, #139378; R8.9, +1.6 *7*, #139377; R21.3, +4.0. *8*, #139380; R9.1, +12.1. *9*, diagram of ventral area and adjoining plates; shaded oval area marks locus of flagellar pore(s).

placed slightly more than one girdle width. Ventral area large, chiefly on hypotheca; some boundaries of constituent plates usually visible. Rupture apparently by separation of plates along sutures in apical region.

*Latin diagnosis.*—Corpus subglobosum; apex obtusus, corpus leviter compressum ab dorso ad ventrem, diametros 25–30$\mu$. Crassitudo thecae minor quam 0.3$\mu$, praesertim parva in regio apicalis. Suturae simplicae, leviter densatae. Formula tabularum: 4′, 4a, 7′, 6g, 6‴, 2p, 1⁗. Tabulae 1–4a magnae et subaequalia, pentagonae; tabulae 1p et 2p magnae, 2p major; tabulae 1″ et 7″, 1‴ et 6‴ minor ceteribus eiusdem ordonis; tabula 1′ incongruens et attingit vix tabulam 7″. Cingulum sinistrum, insolenter latum (5–7$\mu$), amotum parve plus quam latitudo unius cinguli. Regio ventralis magna, pleurumque in hypotheca; sutura circum tabulam inaequalem postremam et partes suturarum circum tabulam intermediam quae apponit tabulam 1‴ plerumque manifestae; limites tabularum ceterarum regionis ventralis interdum manifesti. Abruptio effecta simulate reseratione sutuarum inter tabulae regionis apicalis.

*Types and other material.*—Holotype: USNM 139379; R10.2, +7.1 (pl. 119, figs. 1,2, text-figs. 10,11). The slides containing the holotype and all figured paratypes have been deposited in the U.S. National Museum whose catalog numbers appear in the explanations of illustrations, along with the coordinates* of individual specimens.

*Occurrence.*—Lower Jurassic, Lias alpha, zone of *Schlotheimia angulata*. Core sample of medium gray non-calcareous shale from a depth of 4702–4722 feet in the Danish American Prospecting Company's Gassum No. 1 well, 10 km. north of Randers, Jutland, Denmark. Geographic coordinates of well: 56° 34′ N. Lat., 10° 02′ E. Long. Top of Lias alpha is at about 4633 feet and the zone extends to about 4964 feet.

*Discussion.*—This small but distinctive species occurs prolifically in the sample studied. In addition to single specimens, groups of a few (pl. 119, fig. 3) to a few tens of specimens are common in the insoluble residues, and large matted masses containing over 200 individuals occur. These are definitely not chains of individuals, but apparently a record of minute sedimentary laminae composed entirely of dinoflagellate thecae.

The specimens are, without exception, compressed into virtually a single plane. Although all directions of compression are recorded, a dominance of compression in a dorso-ventral direction indicates a slight original flattening in that direction. A few specimens flattened in an apical-antapical direction were found, but I saw only one truly lateral compression among hundreds of specimens.

Most specimens reveal only a small part of the tabulation because of the extensive wrinkling of the thin theca and the splitting that often distorts the margins of the flattened specimens. The same features make impossible the accurate measurement of overall dimensions. The thickness of the theca varies from a maximum of about 0.3$\mu$ in the hypotheca to an undetermined minimum in the plates of the apical and anterior intercalary series. The sutures are also less thickened and less distinct apically. No specimen was seen with the epitheca intact. Most specimens show an irregular apical opening (pl. 119, fig. 1; text-fig. 18), apparently formed by opening of the sutures between plates of the apical area (chiefly the apical plates, but also, in part, the anterior intercalary plates), followed by an in-folding or wrinkling of the partially freed plates. This rupture mechanism resembles that known in modern *Gonyaulax* and *Spiraulax* (e.g. Kofoid, 1911), rather than that common among many fossil dinoflagellates, in which a specific plate or group of plates of the epitheca is completely released.

All the factors mentioned above combine to make determination of the apical tabulation especially difficult. (Pl. 119, figs. 4,5 and text-figs. 12,13 illustrate the most nearly complete epitheca observed.) Nevertheless, the great abundance of specimens in varied orientations made it possible to work out the entire tabulation. Even the large ventral area shows distinct traces of tabulation in many specimens (pl. 119, figs. 1,12; text-figs.

* The coordinates measure the position of the specimen in millimeters to the right (R) and left (L) and toward the top (+) or bottom (−) of the slide from an index circle engraved near the lower left corner of the cover glass at the center of an "X" in India ink.

5–8). Three of the sutures are most frequently distinct (text-fig. 1). They are: (1) the suture separating the large and irregular posterior plate (itself apparently compound) from the rest of the ventral area (e.g., pl. 119, fig. 13), (2) the suture along the right side of the intermediate plate adjacent to plate 1‴ (e.g., pl. 119, figs. 1,12), and (3) the short spur bordering the same intermediate plate that runs from the corner of plate 1‴ toward plate 7″ (e.g., pl. 119, fig. 12). The precise openings of the flagellar pores have not been observed with certainty. However, they are located in the small oval area near the protruding tip of plate 7″, as indicated by shading in text-figs. 5,8, and 9.

The distinctive tabulation is adequately shown in the illustrations, but two points merit emphasis:

1. The girdle is relatively wide, nearly as wide as the length of the sutures between adjoining plates of the pre- and postcingular series. Therefore, cursory glimpse of a specimen in equatorial view (especially when the apex and antapex are infolded) seems to show a theca divided into three, subequally wide, transverse rows of plates (suggested by pl. 119, fig. 9, a specimen in which the poles are not infolded).

2. The outline shape of the specific major plates (at least those of the precingular, girdle, and hypothecal series, which can be studied in many specimens) seem to be quite constant, and subject to only slight individual variation. In contrast, the distinctness of the tabulation within the ventral area is highly variable: in some specimens plate boundaries are distinct, whereas in others they are faint or not visible at all, even with the most favorable (phase contrast) illumination.

*Comparison: Dapcodinium priscum* differs in tabulation from all other described dinoflagellates known to me, both modern and fossil. The closest similarity is with *Sphaerodinium* Woloszynska, a modern fresh-water genus with tabulation of 4′, 4a, 7″, 6‴, 2⁗. The epithecal tabulation in the two genera is the same. The hypotheca of *Dapcodinium* differs in possessing two intercalary plates and one antapical plate in contrast to the two similar antapical plates in *Sphaerodinium*. In addition, the ventral area in *Dapcodinium* is larger than in *Sphaerodinium*. The theca of *Sphaerodinium* ruptures along the girdle.

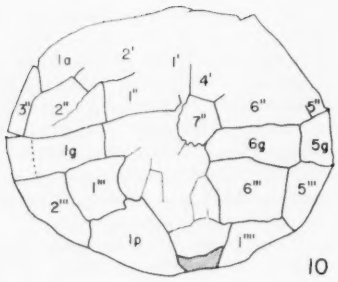
*Systematic position and significance: Dapcodinium priscum* is by far the oldest dinoflagellate whose tabulation has been established. Therefore, it has special interest for the light it may throw on the early evolutionary history of the tabulate group. Two general conclusions seem justified from the present analysis of this species:

1. The early occurrence of a dinoflagellate with the morphology of *Dapcodinium* is consistent with the general picture of dinoflagellate evolution that has emerged from comparative study of modern types.

2. The occurrence, almost at the base of the Jurassic, of a dinoflagellate with the relatively advanced morphology of *Dapcodinium* implies an important pre-Jurassic history of the dinoflagellates, which is already being confirmed by as yet unpublished reports of Triassic and Late Paleozoic dinoflagellates (F. L. Staplin, pers. comm.).

Publications of the last few years have rapidly expanded our knowledge of fossil dinoflagellates. If they continue at the recent rate, we will soon know enough to begin thinking about evolutionary lines and trends. Until now, such thoughts have been mostly in the realm of fancy, simply because we had not seen enough fossils. From studying modern dinoflagellates, neotaxonomists had concluded that the typically non-thecate Gymnodiniales gave rise to the typical thecate Peridiniales. Primitive traits among the Peridiniales are thought to include: (1) a relatively large number of plates, (2) variation in the shape of individual plates, and (3) irregular arrangement of plates. *Glenodiniopsis* and *Sphaerodinium* are modern genera with these characteristics. According to Woloszynska (1917) and, following her, Schiller (1937) and others, they bridge the gap from the more primitive Gymnodiniales to the more advanced Peridiniales. They are both customarily assigned to the Peridiniales, although their tabulation becomes visible only with staining. The less regular tabulation of *Glenodiniopsis* marks it as the more primitive of the two.

By such reasoning, the tabulation of *Dapcodinium* would place it between *Glenodiniopsis* and *Sphaerodinium*, but closer to the latter, from which it differs only in the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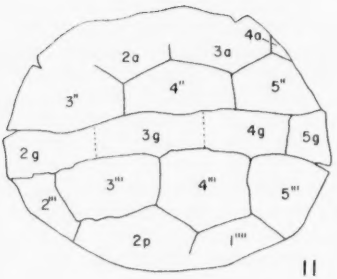
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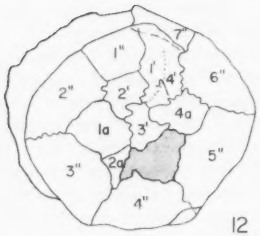
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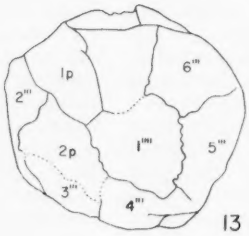
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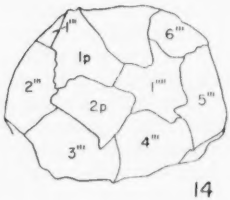
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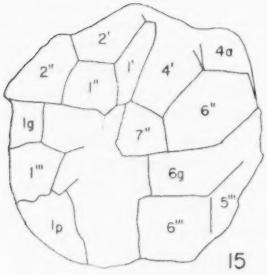
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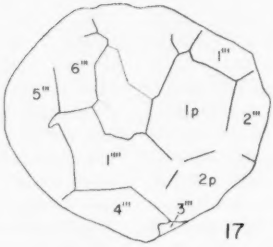
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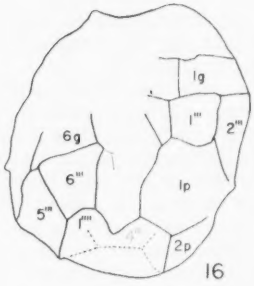
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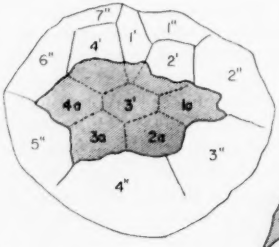
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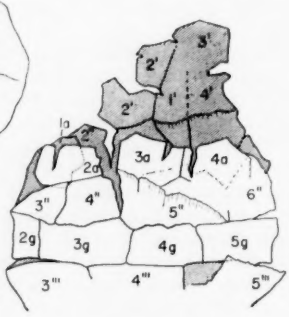
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ventral area and near the antapical pole, as noted above. Of course, we cannot judge with certainty whether the sutures of *Dapcodinium* were visible *in vivo*. It is possible that some of those in the thin-walled apical region may not have been visible. Perhaps they have been accentuated by fossilization. However, some of the sutures are thickened or slightly raised in the fossils, and so probably would have been discernible in living specimens.

It appears, then, that *Dapcodinium* in the Lower Jurassic was a genus already far advanced beyond the most primitive stages of dinoflagellate development as deduced from the study of modern specimens. The genus may be considered a relatively primitive representative of the Peridiniales. However, its complexity leads us to conclude that the dinoflagellates had a pre-Jurassic history that was extensive, at least in terms of morphological differentiation, although we cannot yet guess its time duration.

*Associated microfossils:* Next to the specimens of *Dapcodinium*, which are the most abundant objects and the only dinoflagellate in the preparations, disaccate conifer pollen of several types dominates the assemblage of acid-insoluble microfossils. Other, relatively minor constituents, include occasional *Micrhystridium*, pollen of cycadaceous and tsugoid types, *Classopollis*, and a few trilete spores (*Reticulatisporites*, *Gleicheniidites*, *Deltoidospora*). Conifer tissue fragments are also common.

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MANUSCRIPT RECEIVED AUGUST 22, 1960

(*Explanation of Plate 119 will be found on page 1002*)

TEXT-FIGS. *10–20*—*Dapcodinium priscum* n. gen., n. sp. Camera lucida drawings; ×1250 except 12 and 13. *10,11*, holotype (#139379; R10.2, +7.1), ventral view focused on ventral and dorsal surfaces. *12,13*, paratype (#139377; R6.4, +9.7), apical view focused on epitheca and hypotheca; specimen complete except for opening in epitheca where plate 3a and part of 2a are missing or turned under; suture between plates 1′ and 4′ not visible; ×1500. *14*, paratype (#139382; R5.6, +13.8), hypotheca seen from apical direction, showing relationships of 1p, 2p and 1′′′′ to plates of postcingular series. *15*, paratype (#139381; R28.3, +6.4), dorsal view focused on ventral surface, showing relationships of plates 1′, 1′′ and 7′′. *16*, paratype (#139382; R3.4, −0.4), ventral view of distorted specimen showing plate 1′′′′ and adjoining plates; dashed lines show sutures on under surface of specimen. *17,18*, paratype (#139382; R0.1, +11.9), antapical views focused on hypotheca and epitheca; hypotheca shows relation of plates 1p, 6′′′ and 1′′′ to antapical portion of ventral area with its large posterior plate(s); epitheca shows irregular apical opening formed by loss and/or infolding of anterior intercalary plates and portions of apical plates; dashed lines show approximate positions of original plates. *19,20*, paratype (#139378; R10.3, +6.0), specimen with epitheca ruptured along sutures between apical and intercalary series; apical plates 1′–4′ (partly torn) are spread out in continuation of ventral surface. *19*, dorsal view focused on ventral surface, showing also plates 1′–4′. *20*, dorsal view, showing apical plates and portion of ventral surface projecting from beneath dorsal surface bearing plates 2a–4a.

EXPLANATION OF PLATE 119

*Dapcodinium priscum* n. gen., n. sp. Lower Jurassic (Lias alpha), 10 km. north of Randers, Jutland, Denmark. All phase contrast photomicrographs, ×1000 except as noted.

FIGS. *1,2*—Holotype (#139379; R10.1, +7.1) in dorsal view focused on ventral and dorsal surfaces; ×1150. See text-figs. 10,11.

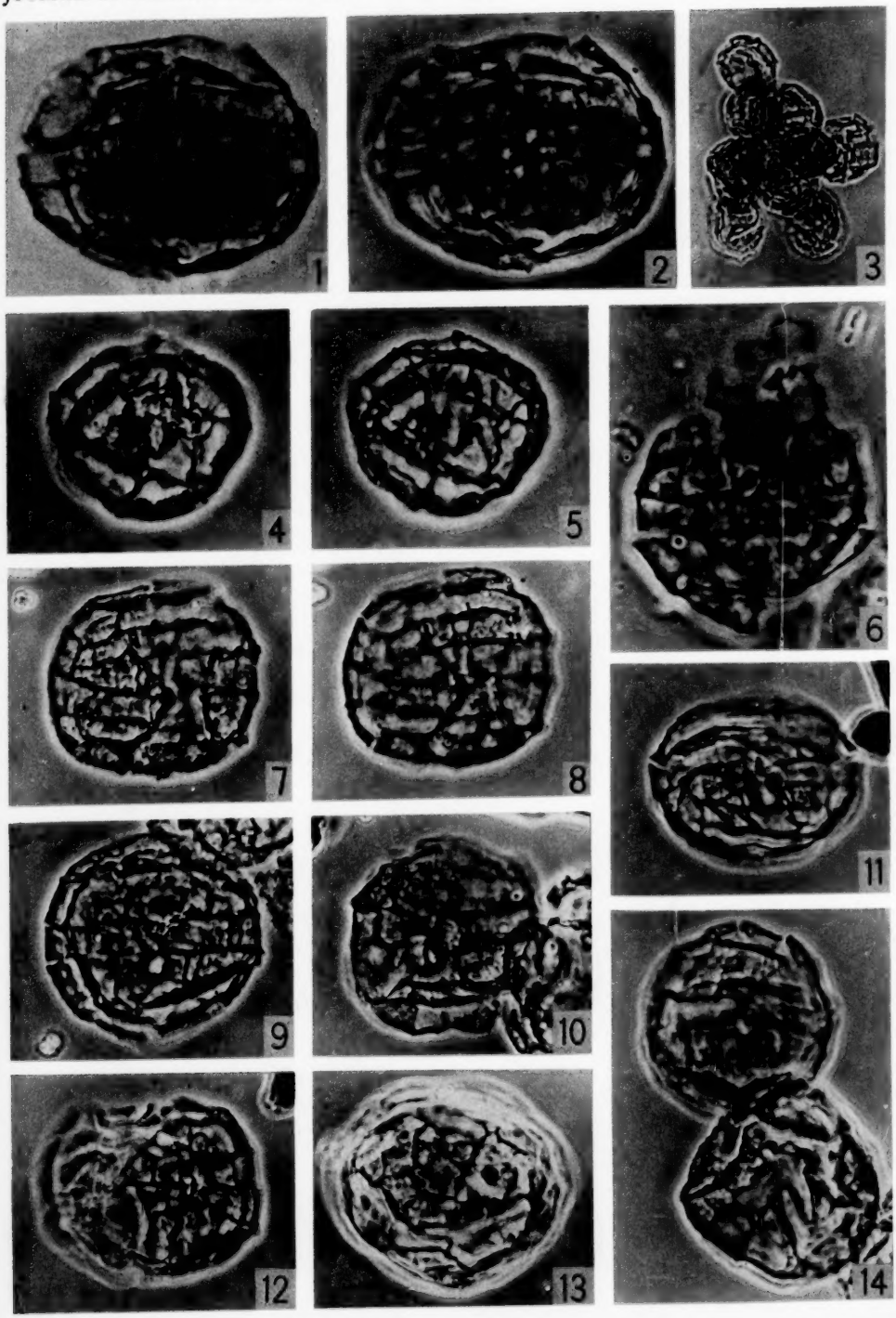
*3*—Cluster of ten specimens (#139376; R17.7, +3.7); ×400.

*4,5*—Paratype (#139377; R6.4, +9.7) in apical view focused on epitheca and hypotheca; ×1250. See text-figs. 13,12.

*6*—Paratype (#139378; R10.3, +6.0), a specimen ruptured along apical limits of anterior intercalary plates, seen in dorsal view focused on dorsal surface; apical plates are spread out toward top as extension of ventral surface; ×1150. See text-fig. 20.

*7,8*—Paratype (#139379; R15.1, +10.8) in slightly oblique ventral view focused on ventral and dorsal surfaces. Pentagonal 4a shows in upper left of fig. 7 and rectangular *3‴* with large 2p below it in fig. 8.

*9–14*—Paratypes. *9*, dorsal view (#139378; R7.4, +5.5) focused on dorsal surface. *10*, dorsal view (#139381; R28.3, +6.4) focused on ventral surface; see text-fig. 15. *11*, dorsal view (#139377; R21.3, +4.0) focused on ventral surface; see text-fig. 7. (reversed). *12*, ventral view (#139380; R9.1, +12.1) focused on ventral surface; see text-fig. 8. *13*, apical view (#139382; R0.1, +11.9) focused on antapico-ventral surface of hypotheca; ×1100; see text-fig. 17. *14*, two specimens (#139379; R20.3, +9.3), parts of apical and anterior intercalary plates visible at top of upper specimen.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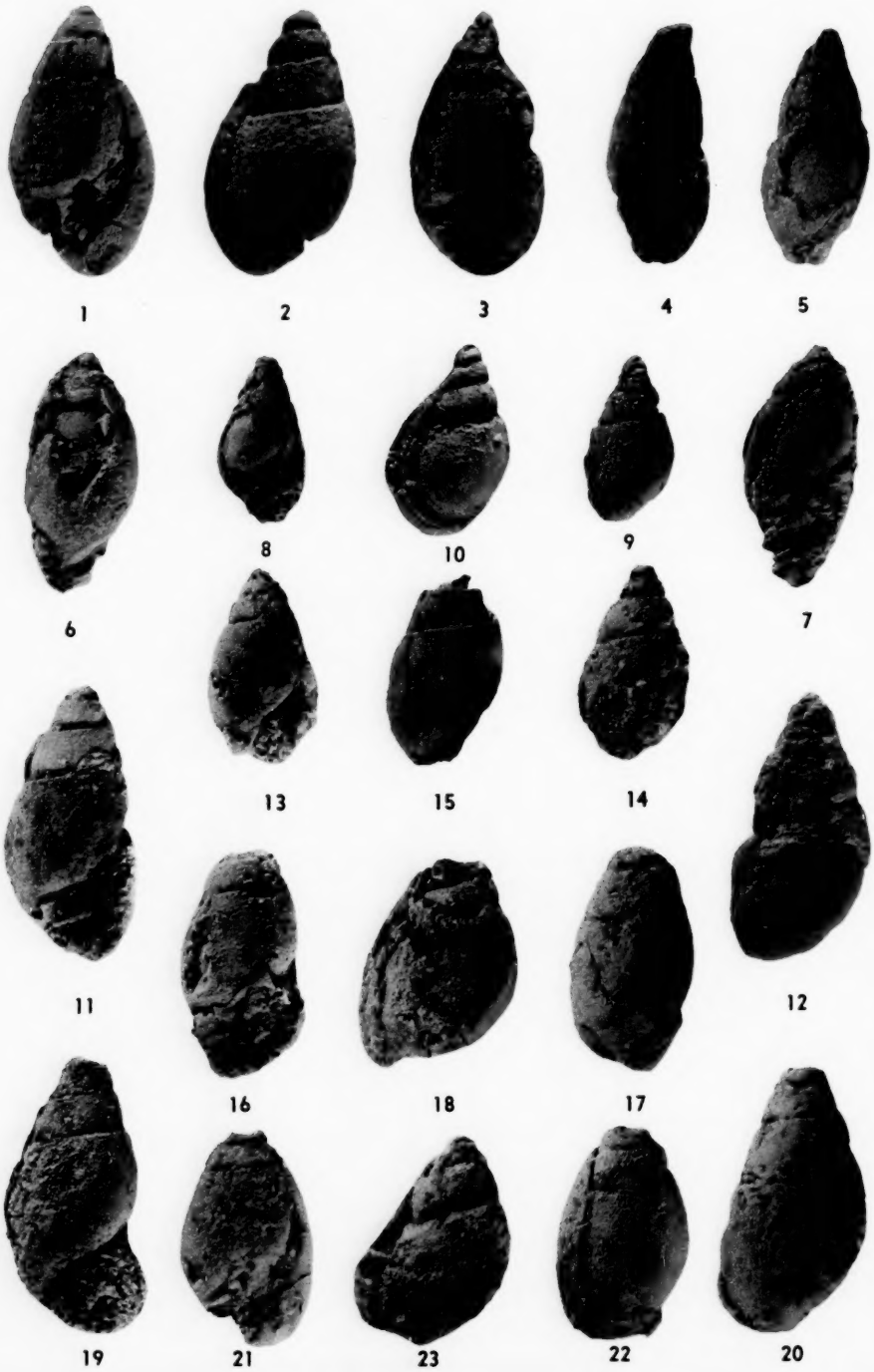
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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1003–1013, PL. 120, 2 TEXT-FIGS., SEPTEMBER, 1961

# NEW SPECIES OF *RINGICULA* FROM THE UPPER CRETACEOUS OF HUERFANO COUNTY, COLORADO, AND REMARKS ON THE "PUGNELLUS SANDSTONE" (CODELL SANDSTONE MEMBER, CARLILE SHALE)

ERLE G. KAUFFMAN AND JOHN K. POPE
U. S. National Museum, Washington, D. C. and Miami University, Oxford, Ohio

(*Abstract will be found on next page*)

## INTRODUCTION

THE "Pugnellus sandstone" (Middle Turonian age) in Huerfano Park, south-central Colorado, contains one of the largest gastropod faunas known from the Upper Cretaceous deposits in the Western Interior of the United States. This unit consists of 20 to 40 feet of massive, buff, tan, and gray, fine-grained sandstone and thin-bedded to platy, sandy shale near the top of the Carlile shale. The fauna is extensive and well preserved. It occurs almost exclusively in small lenses of dense calcareous sandstone within the main sandstone unit.

Gastropods, normally an uncommon group of animals in the Upper Cretaceous sediments of the Western Interior, dominate in abundance and number of species the fauna of over 60 invertebrate species. In numbers, gastropods form 80 to 95 percent of the fauna in different lenses. *Pugnellus fusiformis* (Meek) constitutes 52 to 91 percent of all fossils in any one lens. Species of small gastropods are abundant in the "Pugnellus sandstone," but none have received adequate study. Among these are the two new species of *Ringicula* (*Ringicula*) herein described and illustrated. Pelecypods, prin-

EXPLANATION OF PLATE 120

(all figs. ×7.5)

FIGS. *1–3,6–22*—*Ringicula* (*Ringicula*) *codellana*, n. sp. *1,2*, Apertural and lateral views of the holotype (UMMP 32225), the most complete specimen, showing the characteristic features of the species. *3*. Apertural view of a paratype (UMMP 36981) with a subacute spire and well defined columellar plications. *6,7*, Lateral and apertural views of a paratype (UMMP 36983) with an unusually short spire and well defined columellar plications. *8,9*, Apertural and lateral views of a small individual (UMMP 36985) with flattened rim on posterior portion of whorls near suture. *10*, Lateral view of well preserved paratype (UMMP 36982) showing strong growth lines on outer lip and encroachment of lip onto antepenultimate whorl. *11,12*, Apertural and lateral views of a large paratype (UMMP 36987) with unusually high spire, showing character of an internal mold. *13,14*, Apertural and side views of a small paratype with well defined flat rims at the sutures (UMMP 36989). *15*, Side view of an incomplete paratype (UMMP 36984) showing smooth shell surface, faint growth lines, and character of the suture and rim. *16,17*, Apertural and side views of a medium size paratype (UMMP 36986) with typical smooth shell surface, well defined columellar plications. *18*, Side view of a fragmental specimen (UMMP 36991) with the outer lip extending to the antepenultimate whorl. *19,20*, Apertural and side views of a large paratype (UMMP 32226) with flanks that are flatter than normal and only moderately incised sutures. Aperture incomplete. *21,22*, Apertural and side views of a medium size paratype (UMMP 36988) with well defined growth lines on inner and outer lips.

*4,5*—*Ringicula* (*Ringicula?*) *angusta* n. sp. *4*, Apertural view of the holotype showing slender shape of shell, elongate aperture, 3 columellar plicae, smooth surface with very faint traces of revolving lines, and character of suture (UMMP 36993). *5*, Side view of the holotype showing high spire.

*23*—*Ringicula* sp. A. *23*, Side view of only specimen showing short, broad nature of shell, outer lip extending well onto antepenultimate whorl, and inclination of suture to axis of coiling (UMMP 36992).

ABSTRACT—Two new species of *Ringicula* (*Ringicula*), *R. codellana* and *R. angusta*, and a third distinct form, *R.* sp. A, occur in the "Pugnellus sandstone" of Huerfano Park, south-central Colorado. These are the first representatives of *Ringicula* noted from the Colorado group of the Western Interior. The denticulate inner edge of the outer lip on *R. codellana* indicates that this species, and possibly all three forms, belong to the subgenus (*Ringicula*). They are all atypical of this subgenus in being elongate and smooth shelled. The presence of *Ringicula* in the "Pugnellus sandstone" fauna reinforces the sublittoral, semitropical to tropical ecological assignment of this assemblage.

In Huerfano Park, as at the type area, the Carlile shale is divisible into the Fairport, Blue Hill, and Codell members, in ascending order. The Codell member in Huerfano Park consists of a lower sandstone unit, the "Pugnellus sandstone," of late Middle Turonian age (zone of *Collignoniceras hyatti*) and middle limestone and upper shale units of early Upper Turonian age (zone of *Prionocyclus wyomingensis*). The upper shale is discontinuous, and is an unusual feature of the Codell member. Throughout much of its range in Colorado and Kansas, the Codell member has yielded only an Upper Turonian fauna which occurs in limestone and calcareous sandstone near the top of the section. On the basis of its fauna, some authors have correlated the "Pugnellus sandstone" with the late Middle Turonian Blue Hill shale. Others have correlated it with the lithologically similar sandstones of the lower Codell member. We favor the latter interpretation and present evidence that the lower sandstone unit of the Codell member is of late Middle Turonian age over much of central and south-central Colorado.

cipally species of *Ostrea*, *Inoceramus*, *Mactra*, and *Cardium* are common. Ammonites (predominantly *Collignoniceras hyatti*), bryozoans, annelids, echinoids, crabs, and vertebrates occur as minor faunal elements. In general, the fauna and sediments indicate the presence of an inner sublittoral, subtropical, marine environment during upper Carlile time in south-central Colorado.

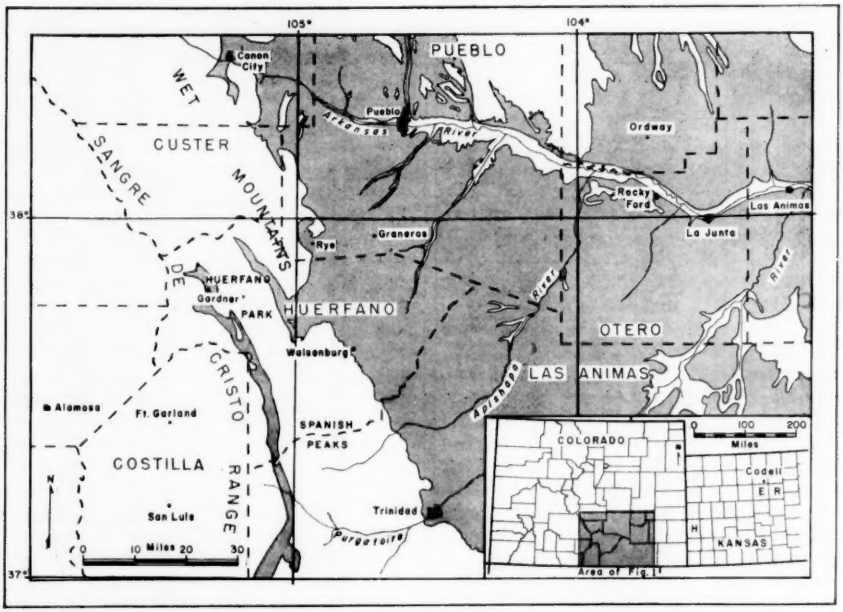
The "Pugnellus sandstone" was first defined and studied in detail by T. W. Stanton (1893, p. 28) who described a fauna consisting of 43 species from it. This unit is of particular stratigraphic interest in that it contains a late Middle Turonian fauna (zone of *Collignoniceras hyatti*) which is also characteristic of the Blue Hill shale member. The "Pugnellus sandstone" is, however, lithologically identical and laterally continuous with the Codell sandstone member of western Kansas and eastern Colorado, considered to be of early Upper Turonian age (zone of *Prionocyclus wyomingensis*) by Cobban & Reeside (1952, chart 10b). In view of the fauna contained in the "Pugnellus sandstone," Cobban & Reeside (1952, p. 1018) and later Reeside (1957, p. 523) correlated it with the Blue Hill member. Briggs & Goddard (1956, p. 42) and R. B. Johnson (1959, p. 98,99) considered it equivalent to lithologically similar sandstone within the Codell member. The lateral equivalents of the "Pugnellus sandstone" are thus controversial, and will be subsequently discussed.

We made collections of the extensive invertebrate fauna of the "Pugnellus sandstone" from 47 different exposures during the summers of 1954, 1958, and 1959. This project was conducted as graduate research under the guidance of staff members of the Department of Geology, University of Michigan. We are indebted to Dr. Norman F. Sohl of the United States Geological Survey, Washington, D. C., for his kind assistance in this project. Dr. Robert V. Kesling and Dr. Louis I. Briggs of the Department of Geology, University of Michigan, reviewed the manuscript and offered helpful criticism. All specimens described in this report are catalogued and deposited in the Museum of Paleontology, University of Michigan (UMMP).

## REGIONAL STRATIGRAPHY

The lower part of the Colorado group (Benton shale of many authors) consists of three well defined formations in Colorado and Kansas. In ascending order, these are the Graneros shale, Greenhorn limestone, and Carlile shale. In eastern Colorado and western Kansas, the Carlile has been divided into three lithologically distinct members, in ascending order, the Fairport chalky shale Blue Hill shale, and Codell sandstone (text-fig. 2).

The basal Fairport member (Rubey &



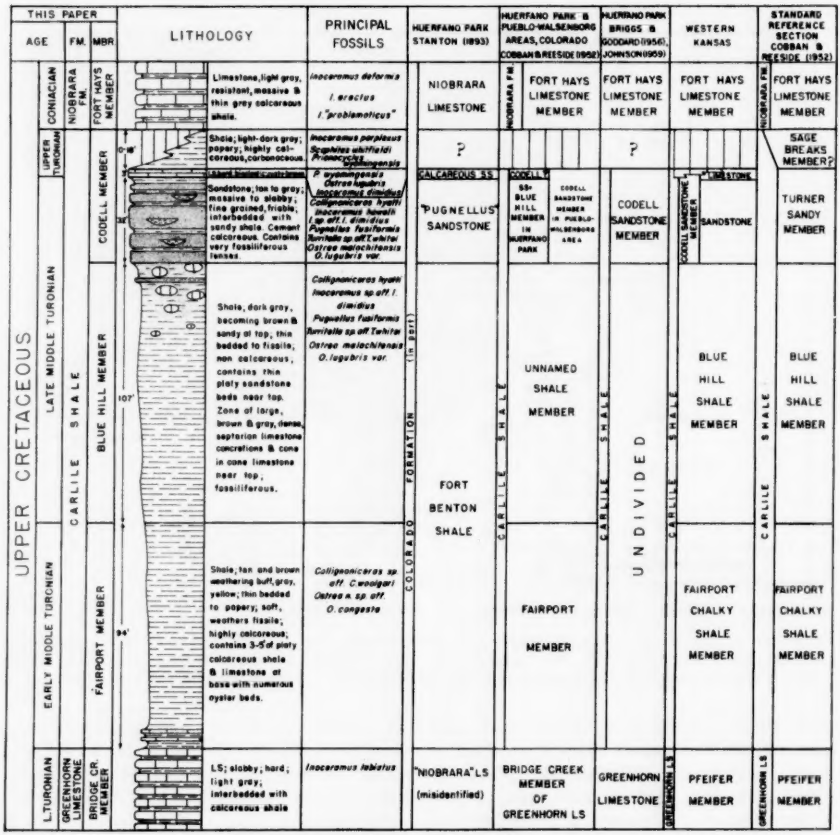

TEXT-FIG. *1*—Huerfano Park, Colorado, and surrounding area. Stippled areas show Cretaceous at surface. On insert map, "E," "H," and "R" are, respectively, Ellis, Hamilton and Russell Counties, Kansas. Note that only the western part of the state of Kansas is shown on the insert map.

Bass, 1925) consists of soft, gray, buff, and tan, thin-bedded, highly calcareous shale or marl. Commonly, interbedded platy to slabby limestone or chalk beds appear in the lower third of the member. These contain extensive beds of oysters closely allied to *O. congesta* Conrad ("Ostrea beds" of early Kansas workers). The Fairport is characterized by the ammonites *Collignoniceras woollgari* (Mantell) and *Scaphites larvaeformis* Meek and Hayden.

The middle member, the Blue Hill shale (Logan, 1897, 1899, Dane & Pierce, 1933), is composed largely of dark gray to blue-gray, non-calcareous, fissile shale which is silty and sandy toward the top. Concretions are common at many levels. The most characteristic of these are large septarian limestone concretions which are generally restricted to the upper part of the member. *Collignoniceras hyatti* (Stanton) and *Scaphites carlilensis* Morrow are important ammonite indices.

The top of the Carlile formation consists of 2 to 40 feet of gray, buff, and tan, fine- to medium-grained, slabby to massive sandstone throughout much of western Kansas and eastern Colorado. This is commonly capped by a thin (1–4 feet), dense, sandy limestone bed. Together, these constitute the Codell member as typically developed. Units of the Codell member show considerable lateral variation and locally one or the other may be missing or much reduced. Consequently, the term Codell has come to have a wide range of connotations.

The Codell sandstone bed was first described by N. W. Bass (1926, p. 28,64) as 20 to 25 feet of sandstone and sandy shale at the top of the Blue Hill shale in western Kansas (Russell, Ellis, and Hamilton Counties: see text-fig. 1). It was named from excellent exposures in bluffs along Saline Valley in Ellis County, Kansas, 5 miles south and a little west of Codell. The term Codell was first applied in Colorado by Mather, Gilluly, & Lusk (1928) to 3 to 20 feet of




TEXT-FIG. 2—Stratigraphic relationships and principal fossils of the Carlile shale in Huerfano Park, Colorado, and surrounding area.

sandstone at the top of the Benton shales in eastern Larimer County (= Niobenton of oil geologists). In this report, the Codell was first designated as a member of the Benton sequence. Dane & Pierce (1933) also recognized the Codell as a member (of the Carlile shale) and restricted the Blue Hill member to the underlying concretionary shales (lower Blue Hill shale of previous reports).

In their study of the Upper Cretaceous stratigraphy north of the Arkansas River in eastern Colorado, Dane, Pierce, & Reeside (1936, p. 216–220) treated the Codell member in considerable detail. The great variability which they noted in the Codell of this region is typical of the unit throughout its range. Sandy shale, sandstone, and limestone (at the top) are all present in the Codell as defined by these and other authors.

Dane, Pierce, & Reeside included in the Codell member all sandy deposits occurring above typical Blue Hill shale and overlying a zone of septarian limestone concretions commonly found at the top of the unit. Following the lead of earlier authors, they placed within the Codell member thin, dense, locally sandy limestones at the top of the sand sequence. These limestones are

remarkably persistent over much of western Kansas and eastern Colorado, and are the sole representatives of the member where the sandstone units pinch out locally along the Front Range of the Rocky Mountains.

In distinguishing the Codell member, most authors have given preference to lithology rather than fauna. The early Upper Turonian age assigned to the Codell member in eastern Colorado and western Kansas is based almost entirely on fossils obtained from the upper limy beds and on its stratigraphic position above the Blue Hill shale (zone of *Collignoniceras hyatti;* late Middle Turonian; Cobban & Reeside, 1956, chart 10b). Typically the bulk of the Codell member, were fully developed, is sparsely fossiliferous or altogether barren. Only the upper few feet of the member containing the dense limestone unit or equivalent calcareous sandstone or sandy limestone yield an extensive fauna. This fauna is characterized by *Prionocyclus wyomingensis* Meek, *Ostrea lugubris* Conrad, and numerous shark teeth of both the cutting and crushing varieties. *Halymenites major* Lesquereux, a marine algae, is the only consistently abundant fossil in the underlying sandstones.

The correlation of this typical Codell lithology at the top of the Carlile shale and assumption of an early Upper Turonian age for it has been applied throughout much of Colorado and western Kansas, except in Huerfano Park and the northern part of the Raton Basin. In the latter areas, the entire sandstone sequence ("Pugnellus sandstone") has been correlated with the Blue Hill member and is thus considered to be of late Middle Turonian age (Cobban & Reeside, 1952, p. 1018, chart 10b; Reeside, 1957, p. 523).

### THE CARLILE SHALE IN HUERFANO PARK, COLORADO

In Huerfano Park, the Fairport, Blue Hill, and Codell members of the Carlile shale may all be recognized. The Fairport member (average thickness 94 feet) consists of gray to buff calcareous shale and marl containing 3 to 5 feet of slabby limestone at the base. *Collignoniceras woollgari ?* (Mantell) and *Ostrea* sp. aff. *O. congesta* Conrad occur near the base of the member.

The Blue Hill shale has an average thickness of 107 feet. It consists of dark gray to blue-gray, non-calcareous, fissile shale, toward the top becoming sandy and silty. Locally, it contains thin beds of sandstone, 1 to 6 inches thick, scattered throughout the upper few feet of the sequence. A widespread zone of large septarian limestone concretions, lenticular limestone beds, and cone-in-cone limestone occurs in the upper 25 feet of the Blue Hill member. Where the top of the Blue Hill shale is sandy in Huerfano Park, the upper limit of the member is drawn at the top of this concretion zone, or in its absence, at the base of the first sandstone unit over 6 inches thick in the overlying "Pugnellus sandstone." *Collignoniceras hyatti* (Stanton), *Cardium pauperculum* Meek, *Turritella* sp. aff. *T. whitei* Stanton, *Inoceramus* sp. aff. *I. dimidius* White, and beds of *Ostrea malachitensis* Stanton form the typical fauna in these concretions. *Turritella* sp. aff. *T. whitei* is the most common species at almost every locality. In its absence, *O. malachitensis* dominates the fauna.

Above the Blue Hill member, an average thickness of 32 feet of tan, buff and gray, fine- to very fine-grained, calcareous sandstone and sandy shale occurs throughout Huerfano Park. This unit is the "Pugnellus sandstone" as defined by Stanton (1893, p. 28). It is capped by 3 feet of very resistant, rusty-brown, bioclastic limestone, typically composed largely of calcite prisms from the shells of *Inoceramus* and other invertebrates, and containing small amounts of quartz sand. The sand content increases significantly to the southeast in Huerfano Park, locally forming up to 60 percent of the matrix. At some localities, a minor disconformity, evidenced by an undulating contact, a dark red, crumbly clay zone, and sharp changes in lithology and fauna, separates the sandstone and the limestone units.

There is little doubt that this sandstone-limestone sequence is the lithologic equivalent of the Codell member as developed in the Pueblo-Walsenburg area (see Cobban & Reeside, 1952, chart 10b) and elsewhere along the Front Ranges of the Rocky Mountains. It can be traced continuously from Huerfano Park, through southeastern Colorado, and into western Kansas to the type section. It extends north along the Wet Mountain front to Cañon City and the

Arkansas River (including the sections of Dane, Pierce, & Reeside, 1936), and discontinuously as far north as southeastern Wyoming.

However, this section contains two distinct faunas in Huerfano Park. The "Pugnellus sandstone" contains highly fossiliferous, calcareous sandstone lenses throughout, which yield a fauna similar to that in the upper part of the Blue Hill member (zone of septarian limestone concretions). *Collignoniceras hyatti* (Stanton), the main index ammonite for the Blue Hill member, is common in many of these lenses.

The thin limestone at the top of the section contains *Prionocyclus wyomingensis* Meek, *Ostrea lugubris* Conrad, *Inoceramus dimidius* White and numerous shark teeth. Many authors consider this fauna to be typical of the entire Codell member and its northern equivalent, the middle part of the Turner sandy member in South Dakota and Wyoming.

Locally, up to 18 feet of gray calcareous shale of Carlile age overlies this limestone in Huerfano Park. It contains *P. wyomingensis*, *Scaphites whitfieldi* Cobban, *Inoceramus perplexus* Whitfield, *I.* sp. cf. *I. labiatus* (Schlotheim), *Pseudoptera* n. sp., and *Ensis?* sp., a fauna which is related to, but generally distinct from that in the underlying limestone. These indicate an age only slightly younger than the limestone (both are early Upper Turonian), and very different environmental conditions.

In view of the two distinct faunas within the Codell sequence of Huerfano Park, Cobban & Reeside (1952, p. 1018), and later Reeside (1957, p. 523) have correlated the "Pugnellus sandstone" with the Blue Hill member of eastern Colorado and western Kansas. This correlation is based largely on the occurrence of *Collignoniceras hyatti* in both units. In this interpretation, only the thin limestone containing *P. wyomingensis*, and where it is developed, the gray shale sequence overlying it represent the Codell member in Huerfano Park.

Other workers however, notably Briggs and Goddard (1956, p. 42) and R. B. Johnson (1959, p. 98,99), included all sandstone in the upper part of the Carlile shale in Huerfano Park within the Codell member, but made no reference to the faunas. Johnson (1959) described the Codell as consisting of a basal zone of lenticular sandstones overlying a dark shale sequence (Blue Hill shale of this paper), a middle dense, rusty-brown limestone which is laterally persistent, and one or two lenticular sandstone beds at the top of the member. This sequence is not characteristic of the upper Carlile shale in Huerfano Park. In the 47 localities studied by the authors, sandstone does not occur above the limestone (zone of *P. wyomingensis*).

## CONCLUSIONS AND REGIONAL RELATIONSHIPS

There is little doubt that the sandstone-limestone-shale sequence at the top of the Carlile shale in Huerfano Park is of two distinct ages (late Middle and early Upper Turonian) and contains distinct faunas. However, we feel that removal of the sandstone unit from the Codell member and its inclusion in the Blue Hill shale forms an impractical division of the Carlile shale contradictory to the original and generally accepted definition of the Codell member (i.e., sandy lithology). Since the "Pugnellus sandstone" in Huerfano Park is continuous with the Codell sandstones to the east, including the type section, we suggest that it is best at present to include the entire "Pugnellus sandstone" within the Codell member in Huerfano Park, giving full recognition to the two-fold nature of its fauna and age. The only other alternative would be to erect another member within the Carlile and to restrict the Codell member to the sandstone (based on lithologic similarities) or to the limestone-shale sequence (based on fauna). Since the distribution of faunas within the Codell member in eastern Colorado and western Kansas is not well known, we feel that it would not be possible to subdivide this sequence at present because the regional applicability of such a division could not be substantiated on the basis of available evidence.

If the "Pugnellus sandstone" is considered as part of the Codell member, and if the early Upper Turonian age of the Codell sandstone is correctly defined elsewhere in the Western Interior, the relationship between this unit in Huerfano Park and elsewhere is simply one of a regressive sand fa-

cies which first appears in south-central Colorado in the late Middle Turonian and reaches surrounding areas to the north and east by early Upper Turonian time (as proposed by Reeside, 1957, p. 523,524; figs. 11,12). The sandy near-shore facies may thus be traced across time boundaries, as indicated by the sharp faunal change (in particular, ammonites).

However, much of the Codell sandstone below the upper limestone beds in south-central and central Colorado may be of late Middle Turonian age, and fossils will possibly be discovered in the lower part of the section to verify this. The relationships between fauna and lithology described from Huerfano Park are known to exist outside of the park as far north as Cañon City, Colorado (text-fig. 1).

For example, along the east side of the Wet Mountains between the Huerfano River and a point 10 miles north of Rye, Colorado, extensive late Middle Turonian faunas, characterized by *Collignoniceras hyatti* and *Pugnellus fusiformis*, have been collected from sandstone in the upper Carlile shale at four different localities. These sandstones were correlated with the Codell member (before discovery of the Middle Turonian faunas) by Dane, Pierce, & Reeside (1936, p. 216–220) and others. The faunas occur in small, highly fossiliferous, calcareous sandstone lenses from 4 feet below the top of the sandstone sequence to its base. The sandstone at each locality is overlain by a thin, dense limestone containing *Prionocyclus wyomingensis*, *Ostrea lugubris*, and numerous shark teeth (B. J. Gallo, personal communication). The fauna-sediment relationships here are identical to those in Huerfano Park, as two distinct ages for the lower and upper part of the Codell member at both localities are indicated.

Along the Arkansas River west of Cañon City, *Ostrea malachitensis* Stanton, a common Middle Turonian (Blue Hill shale-"Pugnellus sandstone") species in Huerfano Park and near Rye, is locally abundant in the upper part of the sandstone of the Codell member. A thin limestone or calcareous sandstone caps this sandstone unit and bears *Prionocyclus wyomingensis* and *Ostrea lugubris*. Although Cobban & Reeside (1952, chart 10b, p. 1018) defined the range of *O. malachitensis* as limited to the Upper Turonian (lower and middle Turner sandy member of the standard Upper Cretaceous section), this species was originally described from the "Pugnellus sandstone" of Huerfano Park, now considered to be of late Middle Turonian age. In this area, *O. malachitensis* is limited to the Blue Hill shale member and the "Pugnellus sandstone," and does not range up into the zone of *Prionocyclus wyomingensis* (early Upper Turonian). The distribution of *O. malachitensis* observed at Cañon City therefore suggests that the Codell member in that region may also include sediments of two distinct ages.

In conclusion, the Codell member in Huerfano Park, as defined in this paper, consists of a lower sandstone unit ("Pugnellus sandstone") of late Middle Turonian age (zone of *Collignoniceras hyatti*), and an upper limestone and calcareous shale sequence of early Upper Turonian age (zone of *Prionocyclus wyomingensis*). This sequence is laterally continuous and lithologically identical to the Codell member as typically developed in eastern Colorado and western Kansas, including the type section. This correlation is considered practical and valid, especially in view of the generally accepted definition of the Codell member based primarily on sandy lithology. Faunal evidence indicates that the Codell member may include sediments of two distinct ages over a wider area than previously thought in eastern Colorado and western Kansas.

## SYSTEMATIC DESCRIPTIONS

### Superfamily ACTAEONACEA

### Family RINGICULIDAE

Genus RINGICULA Deshayes 1838, p. 342
(=APTYCHA Meek, 1862, p. 90)

*Type species:* by monotypy, *Auricula Rigens* Lamarck, 1799, p. 76.

*Diagnosis.*—Small, depressed conoidal to turreted shells with a short to moderately high spire. Apex blunt to acute. 4 to 7.5 whorls present, moderately increasing in size; body whorl large, its length one-half to two-thirds the total shell length. Protoconch mammillate. Labral outline auriform, expanded anteriorly, contracted posteriorly. Outer lip greatly thickened, with or without denticulate inner margin; lip attenuated posteriorly onto penultimate, and on some

specimens, antepenultimate whorl. Labral profile straight to oblique. Aperture contracted, caniculate posteriorly, expanded anteriorly. Columella short, curved, twisted, in most cases with callus. 2–4 columellar plaits present. Shell smooth, or bearing fine revolving lirae or incised lines. Cretaceous to Recent.

Group I. RINGICULA (RINGICULA s. str.) Morlet

*Diagnosis.*—Outer lip denticulate within.

RINGICULA (RINGICULA) CODELLANA n. sp.
Pl. 120, figs. 1–3, 6–22

*Description.*—Shell very small; outline subconoidal. Spire blunt to subacute, moderately high, equalling one-third to three-fifths the total length of the shell. Apical angle averaging 44°. Protoconch (in the sense of Knight, 1941) very small, subround, gently arched, mammillate. 1 to 1.5 smooth, rounded, moderately convex nuclear whorls present. Apex of spire low and depressed. Total number of whorls 5 to 5.5, moderately increasing in size, with slightly to moderately biconvex profiles. Body whorl large, somewhat inflated, abruptly constricted and terminated anteriorly. Whorls on many specimens with very narrow flattened posterior rim or shoulder near suture. Suture moderately to deeply incised, forming an angle of about 13° with axis of coiling.

Shell smooth, marked only by very fine, crowded, nearly obscure growth lines, their trace unevenly convex toward aperture, with greatest curvature anteriorly. Growth line angle 10 to 14°.

Aperature large, its length about two-thirds the total length of the shell; aperture expanded and rounded anteriorly, narrowly contracted, curved, and attenuated posteriorly. Labial outline greatly varicose. Outer lip somewhat reflected, greatly thickened, thickest medially. Lip narrowly attenuated posteriorly onto posterior margin of penultimate whorl, on some specimens reaching antepenultimate volution. Outer portion of lip with well defined growth lines or fine axial costellae on well preserved specimens (see pl. 120, figs. 10,22). Inner margin of outer lip thickened with callus and denticulate (pl. 120, fig. 1), bearing 10 to 15 low, rounded, node-like denticles which are slightly elongate in the direction of coiling. Anterior portion of outer lip abruptly curved and thinner. Labral profile oblique and slightly arcuate.

Inner lip broad, moderately thickened by callus; outline arcuate, narrowly diverging from outer lip posteriorly, abruptly curved obliquely under body whorl to inner edge of columella, then moderately recurved to meet outer lip in broad shallow anterior canal. Termination of canal with shallow notch. Inner lip on columella bearing 2 relatively large, narrow, elongate plicae between base of body whorl and anterior canal.

Dimensions of holotype, an average size specimen: height 5.5 mm.; width 3 mm.; height of body whorl 3.75 mm.

*Remarks.*—No previously described Cretaceous species of *Ringicula* are closely comparable to this form. It differs from most in lacking revolving ornamentation, in the nature and extent of the aperture, and in having the inner edge of the outer lip denticulate, a character which is not common on smooth shelled forms. In addition, it is more elongate than the majority of Cretaceous species of *Ringicula*. *R. angusta*, n. sp., is much slenderer, with a proportionately higher spire, narrower aperture, nearly flat flanks, and lacks a narrow flat rim anterior to the suture. *R. angusta* has three columellar plicae.

*R. codellana* is an uncommon but widespread component of the gastropod fauna in the Codell, or "Pugnellus" sandstone. It is usually associated with other small gastropods, such as *Cerithioderma occidentalis* (Stanton), young of *Pugnellus fusiformis* (Meek), and *Actaeon propinquus* Stanton. Eleven specimens, some of them complete, have been collected. The trivial name is derived from the stratigraphic unit to which the species is restricted.

*Occurrence.*—Widespread but uncommon in highly fossiliferous, calcareous, sandstone lenses of the "Pugnellus sandstone" (lower Codell member) at several localities in Huerfano Park, Huerfano County, Colorado.

*Types.*—Holotype, an average size, complete, mature shell showing the features of the aperture, UMMP 32225; paratypes, several nearly complete and fragmental, average size to small specimens, UMMP 32226, 36981 to 36991.

RINGICULA (RINGICULA?) ANGUSTA n. sp.
Pl. 120, figs. 4,5

*Description.*—(Based on holotype); shell very small; outline elongate subconoidal. Spire high, narrow, straight sided. Tip missing; apex probably subacute. Height of spire about two-fifths the total shell length. Apical angle 36°. Protoconch and nuclear whorls unknown. Total number of whorls about 5 to 6, possibly 7, increasing moderately in size. Body whorl large, somewhat convex, bluntly terminated and constricted anteriorly. Whorl profile very slightly biconvex. Suture incised, linear, forming an angle of 9° with axis of coiling. Suture not bordered with rim, as in *R. codellana*.

Surface typically smooth, in isolated spots bearing very faint, evenly and moderately spaced, raised revolving lines. Growth lines very fine, moderately spaced to crowded, nearly straight to broadly convex aperturally over most of whorl, more moderately curved on anterior one-quarter of body volution. Growth line angle averaging 9°.

Aperture incompletely known, elongate, narrow, large, equalling about one-half the total shell length; aperture expanded and transversely subovate anteriorly, narrow, curved, and probably attenuate posteriorly. Labral outline unknown. Outer lip broken on both known specimens, apparently thickened, attenuate posteriorly, reaching suture and onto anterior one-half of penultimate whorl, possibly further. Inner lip incompletely known, bearing thick callus on flanks of body whorl. Columella bearing two large, widely spaced, narrow, elongate, converging plicae. A third smaller columellar plication is present between them in the posterior portion of the interspace. Anterior canal broad, shallow, very short, with wide notch anteriorly. Canal situated at junction of outer and inner lips. Shell moderately thin.

Dimensions of holotype, the largest specimen: length of shell 5.2 mm.; spire height 1.8 mm.; width of body whorl 2.4 mm.

*Remarks.*—*Ringicula angusta* is more elongate and has a higher spire than the majority of described Cretaceous species. It appears to be closely related to *R. acutispira* Shumard and *R. subpellucida* Shumard from the Eagle Ford shale of Texas. The former species differs from *R. angusta* in having well developed spiral lines. *R. subpellucida* is broader and has a shorter spire, a thinner outer lip, and a different arrangement of the columellar plicae. *R. angusta* is most closely related to *R. codellana* n. sp., with which it occurs. The two species differ in many respects. On *R. angusta*, the spire is proportionately higher, appears to have been more acute, and the apical angle is narrower than that of *R. codellana*. The entire shell is higher and more slender; the body whorl is less inflated. The sutures are less incised and are not bordered by a narrow flat rim. The flanks of the whorls are notably flatter.

Faint spiral lines are present on parts of the whorls, a feature not present in *R. codellana*, and the growth line angle is slightly smaller. The aperture is narrower, more elongate, and the inner lip more steeply inclined and strongly curved. The columella is more erect, and bears three plicae, compared to two on *R. codellana*. The major plicae on *R. angusta* are widely separated and have a greater angle of convergence than found on the associated species.

Despite these differences, the two species show very close relationships and occur in the same stratum, the Codell sandstone. Only two specimens of *R. angusta* are known.

*Occurrence.*—In small, highly fossiliferous, calcareous sandstone lenses within the major sandstone of the Codell member (= "Pugnellus sandstone"), Carlile shale, in the lower part of the valley of Pantleon Creek, S½ NW¼ sec. 28, T. 26 S., R. 71 W., Huerfano County, Colorado.

*Types.*—Holotype, a small imperfect specimen lacking the apex of the spire, portions of the shell, and the outer lip, UMMP 36993; paratype, a small imperfect shell provisionally assigned to this species (not illustrated), UMMP 36994.

RINGICULA sp. A
Pl. 120, fig. 23

*Remarks.*—The specimen considered here is a small, poorly preserved, fragmental shell of a *Ringicula* with features that distinguish it from both *R. codellana* and *R. angusta*. The shell is short and broad, subconoidal, and has a moderately high, blunt spire. There are 4 to 5 volutions, increasing moderately in size. The body whorl is large and

inflated, and is bluntly terminated anteriorly. The whorl profile is typically moderately biconvex. Most whorls have a narrow but prominent posterior shoulder below the suture. The suture is incised, and inclined to the axis of coiling at 21°. The aperture is poorly known, and the columellar features are not preserved. The shape of the aperture is subround. The outer lip is thickened, reflected, and attenuated posteriorly, extending to the antepenultimate whorl. The anterior canal is very short. The shell is thin, except where callus has been deposited, and smooth.

*Ringicula* sp. A is most closely related to *R. codellana*, but differs from that species in the more robust stature of the shell, the broader posterior shoulder or rim near the suture, the rounder aperture, broader apical angle, and much greater inclination of the suture to the axis of coiling. Although this form differs decidedly from the species with which it occurs, we do not feel that a new species should be erected at present on the basis of the available material.

*Occurrence.*—In highly fossiliferous lenses of the main sandstone unit ("Pugnellus sandstone") of the Codell member, Carlile shale, in an unnamed stream gully 1.3 to 1.5 miles north-northwest of Red Wing, SW¼ sec. 26, T. 26 S., R. 71 W., Huerfano County, Colorado.

*Figured specimen.*—A small imperfect shell lacking the features of the aperture and tip of the spire, UMMP 36992.

## PALEOECOLOGY

Late Middle and Upper Turonian time in south-central Colorado was marked by an abrupt shallowing and restriction of the epicontinental seas that had previously covered most of the Western Interior. Sediments deposited during this time consisted dominantly of sandy clastics. Extensive development of ripple marks, cross laminations, and lenticular bedding suggest a shallow water, near-shore to littoral, marine environment affected by moderately strong currents and wave action. Whether the change from shale to sand deposition was caused by filling of the sedimentary basin or lowering of sea level is a matter of conjecture (Reeside, 1957, p. 524).

The extensive invertebrate faunas associated with these deposits in Huerfano Park are made up largely of shallow water species. About 90 percent of the genera present in these faunas have modern representatives. About 75 percent of modern species of these genera are restricted in their bathymetric distribution to the inner sublittoral and inner neritic marine environments. Most of the remaining species range from shallow to deep water. The majority are tropical to subtropical warm water forms.

Although modern species of *Ringicula* are most commonly found in deep water, many species, in particular those of the Pacific Ocean, inhabit the shallow bottoms of the inner sublittoral zone. Some of the Japanese and Philippine species occur in depths as shallow as 3 to 6 fathoms. Species occurring off the coast of the United States today (North Carolina to the Caribbean) are moderately common in water from 34 to 500 fathoms in depth. Deep water forms are common in water up to 7000 feet, and a few forms are apparently confined to the abyssal regions.

Modern species of *Ringicula* range over nearly all tropical and subtropical seas (Tryon, continued by Pilsbry, 1893, p. 394). Very little has been written concerning the sediment types with which modern species of *Ringicula* are associated, but at least one form, *R. abyssicola* Brazier, is confined to sand and sandy mud at depths of about 30 fathoms, an environment which could easily be represented by parts of the Codell sandstone.

The ecologic ranges of *Ringicula* therefore generally agree with previous interpretations of the Codell sandstone environment based on faunal and sedimentary studies (i.e., warm shallow water near to a shoreline), although shallow as well as deep water forms could be represented in the Codell faunas. The occurrence of 3 distinct members of a genus in a single marine environment is not natural, and if *R. angusta* and *R.* sp. A were native to the sandy Codell environment, one would expect them to be more common. The majority of shells belonging to *Ringicula* in the sandstone are broken and worn, and yet this type of shell, small and heavy, should be resistant to normal forces of abrasion if it were not transported far. The authors propose that

the ringiculid assemblage in the "Pugnellus sandstone" is in part thanatocoenosic, and that at least two forms were reworked into these shallow water deposits from their normal range farther offshore.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1014–1016, PL. 121, SEPTEMBER, 1961

# REDESCRIPTION OF *SYRINGOPORA MULTATTENUATA* McCHESNEY

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ABSTRACT—A neotype of *Syringopora multattenuata* McChesney is designated and described. This species is characterized by thick walls, an axial tube, dessepiments, and absence of septal processes.

## INTRODUCTION

THE widely distributed tabulate coral *Syringopora multattenuata* McChesney is the only syringoporid reported from undoubted Pennsylvanian rocks in North America, although *S. aculeata* Girty, 1899, *S. pennsylvanica* Shimer, 1926, and *S. surcularia* Girty, 1899 have been recorded from the Rundle limestone of Alberta, Canada, which has been assigned to the lower Pennsylvanian by some authors. However, Raasch (1956) assigns the rocks containing these species to the Mississippian. *S. multattenuata* has been reported from Illinois, Kansas, Iowa, Missouri, Nebraska, Texas, and questionably from Nevada and Utah. Many reported occurrences were not verified for this study, but a relatively complete list appears in Bassler's (1950) Faunal Lists and Descriptions of Paleozoic Corals.

McChesney's original description of *S. multattenuata* (1859 [1860], p. 75; reprinted, 1867, p. 2, pl. II, fig. 4) is not available in many libraries and is here quoted in full from the 1867 reprint:

> "This species grows in large clusters of long, slender, more or less flexuous, cylindrical or subcylindrical corallites, which are unequally approximate on account of the flexuosity; at some points in contact and firmly grown together, while at others they are distant one, two, or even three times their diameter. Tubes of connection irregularly distant, moderately slender, and either at right angles or slightly oblique. Surfaces marked by frequent shallow annulations indicating the stages of growth. Diameter of the corallites less than a line."

The original locality was described as the Coal Measures, 8 miles south of Springfield, Illinois. The illustration accompanying the description was a line drawing of the exterior. Meek (1872, p. 144, pl. 1, figs. 5a,b,c,d), Keyes (1894, p. 122, pl. XIV, fig. 6b), and Heritsch (1939, p. 105, taf. 15, fig. 10; taf. 20, figs. 19–21) have also recorded the species and given descriptions and figures.

As the original description and figures are inadequate by modern standards and McChesney's types at the Chicago Academy of Sciences were lost in the Chicago Fire of 1871 (Pers. comm. to J. W. Durham, Feb. 26, 1960 from E. S. Richardson, Jr., Chicago Nat. Hist. Mus.), a neotype for the species is here designated and described. Material for this study was provided by H. W. Scott of the University of Illinois and thanks are due also to R. L. Langenheim, Jr. of the same institution, and to J. W. Durham of the University of California (Berkeley).

*Description.*—Corallum fasciculate and phaceloid, maximum size of specimens available greater than 8 cm. high, 12 cm. long, 9 cm. wide; corallites very long, cylindrical, parallel to subparallel, straight to somewhat flexuous; calices round, 1 mm.–2 mm. deep; corallites almost uniformly 2.0 mm. in diameter (a few as much as 2.2 mm.), as much as 8 cm. long; external epitheca moderately wrinkled, internal wall markedly rough in most corallites; wall thickness 0.25 mm. to 0.37 mm., average 0.32 mm.; corallites with hollow axial tube bordered by dissepiments; dissepiments steeply inclined and convex toward axis of corallite, generally in one or two rows; scattered tabulae within axial tube; where axial tube is not observed in section (due to flexuous corallite tube) apparent tabulae present, average thickness 0.08 mm., spaced as many as 3 per mm.; distance between corallites 0.0–5.0 mm.; connecting tubules irregularly arranged and relatively numerous, from 0.75 mm.–1.15 mm. in diameter; connecting tubules replaced by pores when corallites are in contact; budding occurs with initial growth at base of corallum and at points in

mature portions; no septal ridges or spines observed.

*Type material.*—Neotype (here designated), specimen no. X-1490 (=sp. no. F382), and hypotypes nos. X-1492 (=sp. no. F153), X-1493 (=sp. no. F373), and X-1491 (=sp. no. F388), all in the Paleontological Collections of the Department of Geology, University of Illinois, Urbana, Illinois. The above description is based upon five coralla or fragments of coralla. A transverse and a longitudinal thin section were made from the specimen designated as the neotype. In addition, five thin sections, as well as numerous polished sections, parlodion peels, and a set of serial sections were made from the other specimens.

*Age and occurrence.*—Available information indicates that McChesney's original locality is now submerged under an artificial lake—Lake Springfield. Specimens are from the following localities: F153 has a "Worthen label" and presumably pertains to the Sangamon County collections of the first Illinois Geological Survey. F373, F382, and F388, presumably collected by T. E. Savage in conjunction with field work for the Springfield-Tallula quadrangle, are from Sangamon County; F382 has a more specific locality designation—this specimen is from Crow's Creek, which may be associated with Savage's locality described as Crow's Mill, approximately one-half mile south of Cotton Hill Station on the Illinois Central Railroad in the Divernon quadrangle. This locality is approximately 8 miles south of the center of Springfield and is probably at or near the locality described by McChesney. According to H. R. Wanless (Pers. comm. to R. L. Langenheim, Jr., May, 1960) the limestone described in the Tallula-Springfield Folio (Shaw and Savage, 1913) is probably equivalent to the Macoupin limestone of the upper part of the lower McLeansboro Group and is lower Missourian in age.

*Discussion.*—Comparison with the Meek (1872, p. 144, pl. 1, figs. 5a,b,c,d), Keyes (1894, p. 122, pl. XIV, fig. 6b), and Heritsch (1939, p. 105, taf. 15, fig. 10; taf. 20, figs. 19–21) descriptions and figures reveals that their transverse sections closely resemble that of the neotype. They did not illustrate longitudinal sections, so comparison in this respect is impossible, but Meek's figure of the exterior of the corallum of his specimen shows closer vertical spacing of the connecting tubules. Heritsch's description cites "strong, wedge-shaped spines which occur in corallites where a separation has taken place and where there are no more tabulae [transl. from German]." Spines were not observed in cross-sections of the specimens studied, although, in the longitudinal sections, the rough internal wall gives the appearance of short thin spines. The characters of *S. multattenuata* that distinguish it from all other species of *Syringopora* are the thick wall, lack of septa, and the hollow axial tube bordered by dissepiments.

The axial tube and dissepiments are of special interest. These dissepiments, similar to those found in rugose corals, are not characteristic of tabulate corals. Hill and Stumm (1956, p. F446) state that dissepiments in tabulate corals are small domed plates, usually not inclined, occurring in the coenenchyme (the common marginarium of cerioid forms). In the glossary of morphological terms (*op. cit.*, p. F247) a dissepiment is defined as a "small domed plate forming a cyst-like enclosure in peripheral region of a corallite," and a tabula (p. F251) is defined as a "transverse partition of corallite, nearly plane, or upwardly convex or concave, extending to outer walls or occupying only central part of corallite." It is here suggested that, although dissepiments in rugose corals are morphologically distinguished from incomplete tabulae by inclination and position, in *S. multattenuata* the tabulae have been modified in the presence of an axial tube to form structures which are morphologically indistinguishable from dissepiments of rugose corals. In several corallites horizontal tabulae occur within the axial tube with dissepiments on either side outside of the tube. These tabulae, however, appear to be of separate origin. The presence of an axial tube in syringoporoid corals was thought by Chi (1933, p. 22) to be of sufficient significance to establish the genus *Kueichowpora*. The essential characters of his monotypic genus were the rarity of stolons, bifurcation by budding, and a long, central, open axial tube. Minato (1955, p. 188), in describing a new species assigned to *Kueichowpora*, stated that although *Kueichow-*

*pora* bore considerable resemblance to *Syringopora*, "the essential difference consists in the presence of a hollow tube in *Kueichowpora* which my [sic] be sufficient basis to distinguish this from *Syringopora* in generic rank." Hill and Stumm (*op. cit.*, p. F472) place *Kueichowpora* in synonomy with *Syringopora* and this writer concurs. The axial tube is here considered a character of specific significance only.

*S. multattenuata* is widespread in Pennsylvanian rocks of the United States (Bassler, 1950) and also occurs in the Permian of Spitzbergen (Heritsch, 1939). This writer has also found it in the Wolfcampian of the Arrow Canyon Range, Clark County, Nevada.

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## EXPLANATION OF PLATE 121

FIGS. *1–8*—*Syringopora multattenuata* McChesney (all figures slightly retouched), *1*, transverse section of neotype specimen no. F382 showing thick walls and typical pattern of dissepiments, ×7.33; *2*, longitudinal section of neotype F382 made from parlodion peel, ×1.33; *3*, longitudinal section of neotype F382, ×2; *4*, transverse section of neotype F382, ×1.66; *5*, longitudinal section of neotype F382 showing hollow axial tube bordered by dissepiments, ×9.33; *6*, longitudinal section of hypotype F388, ×2.66; *7*, longitudinal section of hypotype F388 showing corallite with axial tube, dissepiments, and horizontal tabulae within tube, ×6.66; *8*, longitudinal section of hypotype F382 showing well developed dissepiments and budding in mature portion of corallite, ×8.66. All specimens are in the Paleontological Collections of the Department of Geology, University of Illinois, Urbana, Illinois.

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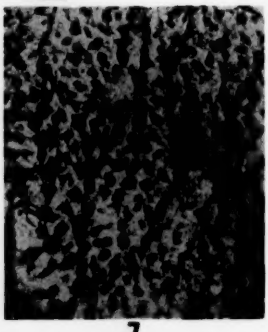

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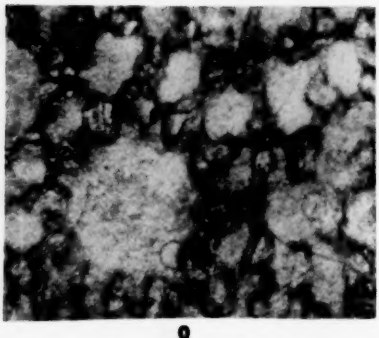

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1017–1019, PL. 122, SEPTEMBER, 1961

# *LISCOMBEA*, A NEW SILURIAN TABULATE CORAL GENUS FROM NEW SOUTH WALES, AUSTRALIA

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ABSTRACT—The new Silurian tabulate coral genus *Liscombea* from New South Wales, Australia, is a heliolitid apparently occupying an intermediate position between the Subfamily Plasmoporinae and the Subfamily Coccoseridinae.

## INTRODUCTION

IN STUDYING the geology of the Liscombe Pools Creek area in which Silurian strata, trending north-south are closely folded and faulted, Stevens (1950) collected small samples of fossils. The material was found in thin bedded fossiliferous limestone and shale lens in a thick sequence of unfossiliferous slate, porphyry, and tuff, cropping out near Liscombe Pools Creek, 18 miles S 38° W from Cowra, New South Wales. The new tabulate genus *Liscombea* occurs in one of the limestone lens in the porphyry and *Halysites* sp. and *Favosites* sp. have been found in shale higher in the succession. The occurrence of *Halysites* sp. (Stevens, 1950) has been taken to indicate a Silurian age. The present paper describes the new genus *Liscombea* and the type species, *L. insolens* sp. nov., which appear to occupy an intermediate position between the Subfamily Plasmoporinae Wentzel 1895 and the Subfamily Coccoseridinae Kiaer 1899.

I am grateful to Miss Helen Duncan, U. S. Geological Survey, Washington, for helpful discussion concerning the new genus.

## SYSTEMATIC PALEONTOLOGY

Order TABULATA Milne-Edwards and Haime 1850

Family HELIOLITIDAE Lindstrom 1876

Genus LISCOMBEA n. gen.

*Type species.*—*Liscombea insolens* n. sp.

*Diagnosis.*—The frondescent coralla have smooth slender cylindrical branches. In the axial regions of the coralla the corallites

## EXPLANATION OF PLATE 122

FIGS. *1–10*—*Liscombea insolens* sp. nov. Silurian. Road cut crossing Liscombe Pools Creek, Parish of Malongulli, New South Wales, Australia.

*1*—Longitudinal section showing thin walled, closely tabulate corallites in the axial region and dense coenenchyme filling the wide intracorallite spaces in the peripheral region. U.S.G.D. 12409. ×22.

*2*—Longitudinal section showing closely tabulate corallites in the axial region and dense coenenchyme in the peripheral region. Holotype, U.S.G.D. 12408. ×12.

*3*—Transverse section showing circular corallites and coenenchymal trabeculae in the axial region and dense coenenchyme in the peripheral reigon. Holotype, U.S.G.D. 12408. ×25.

*4*—Shallow tangential section showing circular calices fringed by tubules and dense coenenchyme filling the intracorallite spaces. U.S.G.D. 12409. ×45.

*5*—External aspect of a colony of slender, cylindrical branches. Holotype, U.S.G.D. 12408. ×1.

*6*—Deep tangential section showing circular corallites and coenenchymal trabeculae piercing the intracorallite spaces. Holotype, U.S.G.D. 12408. ×12.

*7*—Shallow tangential section showing circular calices fringed by 12 tubules. Holotype, U.S.G.D. 12408. ×25.

*8*—Deep tangential section showing circular corallites and numerous coenenchymal trabeculae in the intracorallite spaces. Holotype, U.S.G.D. 12408. ×50.

*9*—Shallow tangential section showing the disposition of calices and coenenchyme along a branch. U.S.G.D. 12409. ×20.

*10*—Portion of a longitudinal section showing abrupt development of dense coenenchyme in the early peripheral region. U.S.G.D. 12409. ×50.

grow steeply inclined to the axes of growth of the branches and curve abruptly laterally in the peripheral region. Intracorallite walls are slender, granular lines in the axial region. Wide intracorallite spaces develop in the subperipheral and peripheral regions and these are filled with dense coenenchymal trabeculae which coalesce to form tubules. A cycle of twelve tubules surrounds each calyx. Tabulae are flat and complete and increase in abundance from the axial to the peripheral region. Septal trabeculae are lacking.

*Remarks.*—The new genus *Liscombea* is proposed for frondescent heliolitids lacking coenenchyme in the axial region. *Liscombea* resembles *Diploepora* Quenstedt 1879 in possessing a peripheral region having considerable development of coenenchymal trabeculae which coalesce to form tubules and twelve distinct tubules surrounding each calyx. It differs from *Diploepora* in lacking coenenchyme in the wide axial region of the branches. It resembles genera belonging to the Coccoseridinae Kiaer 1899 in the strong development of coenenchymal trabeculae, but differs in lacking septal trabeculae. The genus occupies an intermediate position between the Subfamily Plasmoporinae Wentzel 1895 and the Subfamily Coccoseridinae Kiaer 1899. The combination of dense coenenchymal trabeculae and tubules is characteristic of a group of heliolitids occurring in the Silurian.

The generic name is derived from the type locality outcropping near Liscombe Pools Creek.

LISCOMBEA INSOLENS n. sp.
Pl. 122, figs. 1–10

*Holotype.*—University of Sydney, Geology Department No. 12408. Road cut crossing Liscombe Pools Creek, one mile southwest of Malongulli Trignometrical station, Parish of Malongulli, New South Wales. Longitude 148° 40′; latitude 33° 40′. Silurian. Colonies in a medium grey calcilutite.

*Paratype.*—University of Sydney, Geology Department No. 12409. Locality and horizon same as the holotype.

*Diagnosis.*—Species of *Liscombea* having slender frondescent coralla. Wide intracorallite spaces in the peripheral region filled with dense coenenchymal trabeculae. Abundant, flat diaphragms in the axial and peripheral regions.

*Description.*—Coralla are frondescent; smooth slender cylindrical branches (pl. 122, fig. 7). The branch diameter is 2.5 to 3.5 mm.

In longitudinal section in the axial region the long corallites are steeply inclined to the axis of growth of the branches (pl. 122, figs. 1,2). In the outer part of the axial region they curve slightly and then curve abruptly laterally into the peripheral region (pl. 122, figs. 1,2,10). Corallites, 0.18 mm. diameter in the axial region, expand to 0.29 mm. at the periphery. The corallite walls in the axial region are slender and granular. The intracorallite spaces which develop by separation of the corallites are filled with dense coenenchymal trabeculae (pl. 122, fig. 10). Expansion of these intracorallite spaces continues to the periphery of the colony, and the coenenchymal trabeculae, about 0.03 mm. diameter, increase in number and coalesce to form tubules, 0.04×0.05 mm. to 0.11×0.06 mm. in size. In the peripheral region, radius 0.3 mm. on a branch of radius 1.1 mm., the boundaries of adjacent corallites are completely obscured. Complete straight tabulae are abundant in the axial and peripheral regions. In the axial region the tabulae are about a tube diameter apart, and in the peripheral region they increase in number so that they are commonly less than half a tube diameter apart (pl. 122, figs. 1,2,10).

In tangential sections the calices of the corallites are surrounded by narrow rims, about 0.11 mm. wide, and these are fringed by 12 tubules (pl. 122, figs. 3–5,8,9). Deep tangential sections clearly display the coenenchymal trabeculae (pl. 122, figs. 3,4).

In transverse sections the wide axial region is composed of subcircular corallites, slender corallite walls, and numerous coenenchymal trabeculae; the narrow peripheral region is filled with dense coenchymal trabeculae (pl. 122, fig. 6).

*Discussion.*—*Liscombea insolens* is not closely comparable with any previously described species. In the general arrangement of the microstructures in the peripheral region, it is similar to *Diploeporia grayi* Milne-Edwards and Haime 1851, as both species possess calices surrounded by rims and pene-

trated by 12 tubules, and intracorallite spaces densely filled with coenenchymal trabeculae. *L. insolens* differs from *D. grayi* in the absence of coenenchyme in the axial region, and the smaller dimensions of the skeletal microstructures.

*Remarks.*—The species derives its name from the Latin, *insolens*, meaning unusual, and refers to the unusual combination of microstructures.

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# *PTOLEMAIA*, A NEW COLONIAL RUGOSE CORAL FROM THE LOWER PERMIAN OF EASTERN NEVADA AND WESTERN RUSSIA

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ABSTRACT—*Ptolemaia ftatateeta*, n. gen., n. sp., is described from the Lower Permian (Wolfcampian) part of the Ely limestone in White Pine County, Nevada, and of the Bird Springs formation in Clark County, Nevada. Applicable terminology (in part) is discussed. The following species, all from the Lower Permian of the Ural Mountains, are referred to *Ptolemaia: Wentzelella gracilis* Dobrolyubova, *W. grandis* Dobrolyubova, *W. magnifica* Porfiriev, *W. pseudoelegans* Dobrolyubova, *W. pseudoelegans* var. *prismatica* Porfiriev, *W. styllidophylloides* Dobrolyubova, *W. styllidophylloides* var. *radiata* Porfiriev, *W. timorica* var. *intermedia* Porfiriev (elevated to specific rank), and *W.* aff. *indica* Soshkina, Dobrolyubova, and Porfiriev (as *Ptolemaia uralensis*, n. name). *Ptolemaia* is placed in the Aulophyllidae, although it also seems closely allied to the Waagenophyllidae and the Lithostrotionidae.

## INTRODUCTION

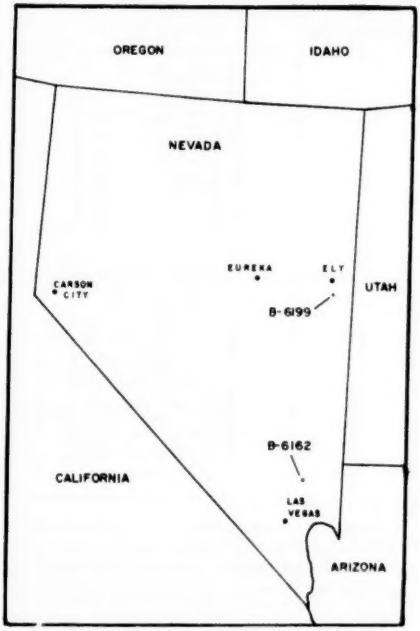
THE Permian colonial rugose coral *Wentzelella* has been reported from Europe, Asia, and New Zealand (Hill 1948, 1957). In the original broad sense, it is here recorded from the Wolfcampian of Nevada (see text-fig. 1). However, recent study has restricted the genus to a relatively few species. The following résumé presents the earlier history of *Wentzelella* and will serve as background for discussion of the further revisions of the genus with which this paper is largely concerned.

## HISTORICAL RÉSUMÉ

Grabau (*in* Huang 1932, p. 46) erected *Wentzelella* for rugose corals having "prismatic corallites in close contact, septa extending to the epitheca without the external zone of vesicular tissue found in *Lonsdaleia*. Columella of the complicated *Lonsdaleia* type." Huang (1932, p. 46) listed *L. salinaria* Waagen & Wentzel (1887, p. 895, pl. C, figs. 1,3,4) as the type. New species and varieties were described by Dobrolyubova (1941, *in* Soshkina *et al.*, p. 187–190,192–195,197–199,263–265, pl. XLIII, figs. 1–3, pl. XLIV, figs. 1,2, pl. XLV, fig. 1, pl. XLVI, fig. 1, pl. XLIX, fig. 1, pl. L, fig. 1, pl. LII, fig. 1), Douglas (1936, p. 24, pl. II, figs. 3,4), Flugel (1955, p. 305–307, tfl. 35, fig. 10), Heritsch (1936, p. 127, tfl. XVIII, figs. 1,2, text-figs. 29–31), Leed (1956, p 19, pl. 5, figs. 1–4), Minato (1955, p. 108–110, pl. 26, fig. 9, text-fig. 8d), Montanaro-Gallitelli (1956, p. 50–52, tav. II, fig. 1), Porfiriev (*in* Soshkina *et al.*, p. 186,190,195–197,199,263–265, pl. XLIII, fig. 1, pl. XLVIII, fig. 1, pl. LI, fig. 1, pl. LIII, fig. 1, pl. LIV, fig. 1), and Yabe & Minato (1944, p. 139, pl. 11; 1945, p. 469–472, figs. 1–5). Leed (1956, p. 17, table 1) also presented a "dichotomous key to species [groups] of *Wentzelella*" based upon the types of dissepimentaria, number of septa, and structure of septa within the dissepimentaria. Fomichev (1953, p. 593) considered *Wentzelella* synonomous with *Protowentzelella* Porfiriev (1941, *in* Soshkina *et al.*, p. 179,262). Hill (1956, p. F309) considered *Wentzelloides* Yabe & Minato (1944, p. 141, pl. XII) a subgenus of *Wentzelella*. *W.* (*Wentzelella*) was defined as cerioid and *W.* (*Wentzelloides*) was differentiated by its partly meandroid form. Hudson (1958, p. 185) revised and redescribed the genus, including it in a new family.

Prior to the study of Hudson (*ibid.*), *Wentzelella*, which had been originally separated from *Lonsdaleia*, was retained in the Lonsdaleiidae, although Wang (1950, p. 213) placed *Wentzelella* and other non-lonsdaleoid genera of the Lonsdaleiidae in a new subfamily, the Waagenophyllinae. Hudson (1958) removed the Waagenophyllinae from the Lonsdaleiidae, placing it in a new family, the Waagenophyllidae, which included a

second (and new) subfamily, the Wentzelellinae. *Wentzelella* was transferred to the Wentzelellinae and restricted to species with three orders of septa. Those species formerly included within *Wentzelella* which had two orders of septa, but no tertiary septa, were placed in a new genus, *Ipciphyllum*, and *I. ipci*, a new species, was designated the type species (*ibid.*, p. 179, pl. 33, figs. 1–3,7,10, pl. 35, fig. 4). For reasons stated below, some of the species formerly included in *Wentzelella* cannot be assigned to *Wentzelella* as revised by Hudson (*ibid.*) or to *Ipciphyllum* (nor can they be included within the Waagenophyllidae). These species were not discussed by Hudson (*ibid.*). Hill (1948, p. 128; 1957, p. P51, P56) previously had pointed out that cerioid corals from the Sakmarian and Artinskian of Russia which were referred to *Wentzelella* represented distinct genera.

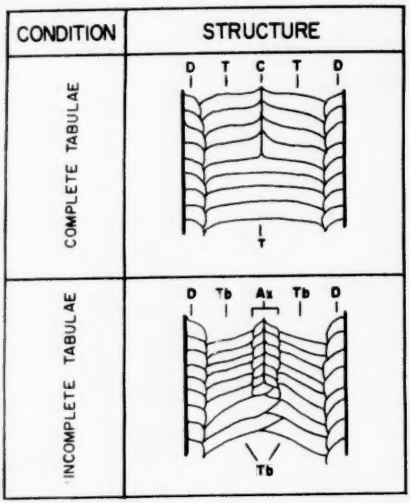



TEXT-FIG. 1—Map of Nevada showing localities where *Ptolemaia ftatateeta* was collected.

## TERMINOLOGY

In his diagnosis of the Waagenophyllidae, Hudson (1958, p. 177) emphasized elements generally observable in vertical section, for which he introduced new structural terminology. *Transverse tabulae* were defined (*loc. cit.*) as "tabulae horizontal or approximately so in tabularium. May be simple or compound, flat, with or without upturned edges, or shallowly curved, proximally or distally, or cystose." *Clinotabulae* were described (*loc. cit.*) as "tabulae, vertical or steeply inclined downwards to axis, usually interseptal. May be simple, flat, or shallowly curved (convex surface towards axis) and continuous with transverse tabulae, or compound or elongate-cystose. May simulate dissepiments." *Clinotabularium* was characterized (*loc. cit.*) as a "tabularium with clinotabulae. Usually forms an outer zone of tabularium adjacent to dissepitheca [a stereozone separating tabularium and dissepimentarium] and often sharply distinguished from an inner (periaxial) zone of transverse tabulae." *Dissepiseptum* was reported (*loc. cit.*) to be a "linear arrangement of small lateral dissepiments replacing septum in dissepimentarium (Douglas 1950, text-figs. 1a,c)." All genera of the Waagenophyllidae were said (Hudson, p. 178) to possess clinotabulae. *Wentzelella*, as revised by Hudson (*ibid.*, p. 185), commonly possesses dissepisepta although *Ipciphyllum* lacks them.

Moore, Hill & Wells (1956, p. F245–251) presented a "glossary of morphological terms applied to corals" in which they defined *tabula* (*ibid.*, p. F251) as a "transverse partition of corallite, nearly plane, or upwardly convex or concave, extending to outer wall or occupying only central part of corallite," *complete tabula* (*ibid.*, p. F246) as a "type consisting of a single platform, not composed of several small plates joined together," *incomplete tabula* (*ibid.*, p. F248) as a "type consisting of several small plates (tabellae) joined together," and *tabella* (*ibid.*, p. F251) as a "small subhorizontally disposed plate in central part of corallite forming part of an incomplete tabula." Thus, although tabula is a structural unit, complete and incomplete tabulae are conditions represented by tabulae and tabellae, respectively (see text-fig. 2). All genera of the Waageno-




TEXT-FIG. 2—Diagrammatic representation showing differences between tabulae and tabellae in rugose corals, with and without axial structure. Ax—axial structure with axial tabellae; C—columella or medial plate; D—dissepiments; T—tabulae, Tb—tabellae.

phyllidae, as defined by Hudson (1958, p. 177) have a complex axial structure containing tabellae and, therefore, cannot have tabulae, in the above sense, but only tabellae in the remaining area of the tabularium. *Clinotabulae*, then, are actually tabellae and the term *clinotabellae* is more appropriate. *Transverse tabellae*, likewise, should be substituted for *transverse tabulae*. Furthermore, the usage of clinotabellae as "continuous with transverse tabulae" (*loc. cit.*) is questionable, since terms for two distinct structures are applied to a single structural unit. A better usage would be to include this type of structure within Hudson's (*loc. cit.*) concept of transverse tabellae "with . . . upturned edges." The only waagenophyllid reported not to have separate clinotabellae was '*Lonsdaleia*' *chaoi Huang var.* [*sic*] (*ibid.*, p. 182–184, pl. 32, figs. 1,2,7–9, text-figs. 2,3) described as having "tabulae . . . horizontal or slightly concave, sharply upturned near dissepimental wall to form clinotabulae" (*ibid.*, p. 184). In such instances there are only two zones of tabellae—axial and periaxial (*i.e.*, transverse), and no third zone of tabellae (clinotabellae), even though the transverse tabellae have upturned edges. This might exclude the species from the Waagenophyllidae but, in fact, the tabularium seemingly contains (*ibid.*, pl. 32, fig. 1) not only axial and transverse tabellae with upturned edges, but also, in places, axial tabellae, flat transverse tabellae, and an outer series of cystose clinotabellae, forming the three zones of tabellae typical for the Waagenophyllidae. *Clinotabellae* should be limited to those structures indicated in the definition of *clinotabulae* by Hudson (1958, p. 177), modified by deleting "and continuous with transverse tabulae." In addition, *clinotabularium*, if defined as "tabularium with clinotabulae" (*loc. cit.*) cannot also be considered identical with a zone of tabularium, as was stated by Hudson (*loc. cit.*). The two usages are contradictory since *tabularium* is defined by Moore, Hill, and Wells (1956, p. F251) as the "axial part of the interior of a corallite in which tabulae [or tabellae] are developed," while a zone of the tabularium is only a part of the tabularium. *Tabularium* has long been such a well understood, generally used, highly utilitarian term, applicable alike to Heterocorallia, Scleractinia, and Tabulata, as well as Rugosa, that it seems unfortunate to modify it for application to a single family.

Except as discussed above, terminology used hereinafter is from Moore, Hill, and Wells (1956, p. F245–F251).

## SCOPE OF STUDY

Published references for 33 species and 3 varieties of *Wentzelella* were examined in the course of this study. *Wentzelella* as revised by Hudson (1958, p. 185) may accommodate *W. canalifera* (Mansuy) (1913, p. 109, pl. XI, fig. 12, pl. XII, fig. 1), *W. molengrafi* (Gerth) (1921, pl. 76, taf. CXLV, figs. 3–5), *W. salinaria* (Waagen & Wentzel) (1887, p. 895, pl. C, figs. 1,3,4), *W. socialis* (Mansuy) (1913, p. 110, pl. XII, fig. 2), *W. szechuanensis* Huang (1932, p. 62, pl. V, fig. 4), and *W. wynnei* (Waagen & Wentzel) (1886, p. 896, pl. C, figs. 5,6). Hudson (1958) did not mention the latter two species. As stated by Hudson (*ibid.*, p. 179–182), species which

may be referred to *Ipciphyllum* are *Wentzelella elegans* Huang (1932, p. 61, pl. IV, figs. 3,4, pl. V, fig. 3), *W. indica* (Mansuy) (1908, p. 54, pl. 14, figs. 1,3), *W. subtimorica* Huang (1932, p. 59, pl. IV, fig. 1), and *W. timorica* (Gerth) (1921, p. 74, tfl. CXLV, figs. 1,2). The affinity of the following species is uncertain because of inadequate published descriptions and/or illustrations: *W. anatolica* Flugel (1955, p. 305, tfl. 35, fig. 10), *W. caracourmensis* (Gerth) (1938, p. 232, tfl. XV, fig. 1), *W. iwaizakiensis* Yabe & Minato (1945, p. 469, figs. 1–5), *W. kitakamensis* Yabe & Minato (1944, p. 139, taf. XI), *W. ozawai* Minato (1955, p. 110, pl. 25, figs. 5,7, pl. 30, fig. 8, text-fig. 8d), *W. paracanalifera* Huang (1932, p. 63, pl. V, fig. 2), *W. sekii* Minato (1955, p. 108,110, pl. 26, fig. 9, text-fig. 8d), *W. stillei* Heritsch (1936, p. 127, tfl. XVIII, figs. 1,2, text-figs. 29–31), and *W. yokoyami* (Ozawa) (1925, p. 72, pl. XIII, figs. 5,6). The following were probably erroneously assigned to *Wentzelella*: *W. harrisoni* Douglas (1936, p. 24, pl. II, fig. 4)—partly thamnasteroid, *W. maoria* Leed (1956, p. 19, pl. 5)—partly thamnasteroid, *W. persica* Douglas (1936, p. 24, pl. II, fig. 3)—largely lonsdaleoid and referred to *Wentzellophyllum* Hudson (1958, p. 186) by Hudson (*loc. cit.*), and *Wentzelella salinaria var. sicula* Montanaro-Gallitelli (1956, p. 50–52, tav. II, fig. 1)—partly thamnasteroid. Leed (1956, p. 17) considered *Lonsdaleiastrea typica* Gerth (1938, p. 232, tfl. XV, fig. 7) a *Wentzelella*, but it is partly thamnasteroid and the original identification is therefore probably correct. No reference or other citation was found for two species mentioned by Fomichev (1953, p. 592). They are *W. incerta* Zhizhina and *W. dobrolyubovae* Zhizhina.

Seven species are not referable to any of the above genera and for them the new genus *Ptolemaia*, with *P. ftatateeta, sp. nov.* as type, is here proposed. The description follows. Systematics are after Hill (1956).

ACKNOWLEDGMENTS

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## SYSTEMATICS

Phylum COELENTERATA
Class ANTHOZOA
Order RUGOSA
Suborder STREPTELASMATINA
Superfamily ZAPHRENTICAE
Family AULOPHYLLIDAE Dybowski 1873
Subfamily YATSENGINAE Hill 1956
Genus PTOLEMAIA, n. gen.

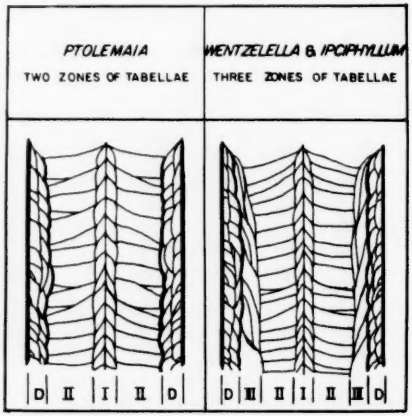
*Diagnosis.*—*Ptolemaia* is a cerioid aulophyllid without fossula and with two orders of septa, minor septa variously developed, well-defined clisiophylloid axial structure, regular dissepimentarium, tabellae of two ranks—axial and periaxial—both of which slope in and up toward the medial plate.

*Description.*—Corallum massive and cerioid; corallites polygonal; septa of 2 orders, rarely lonsdaleoid, dilate or thin in tabularium; major septa well developed, usually less than 25 in number, generally withdrawn from axis; minor septa short and well developed to absent; axial structure clisiophylloid (commonly touching cardinal or counter septa in youth) with well-defined medial plate, septal lamellae and tabellae. Dissepimentarium well developed, generally narrow with 1 to 5 rows of concentric, cystose dissepiments; tabellae of 2 ranks, axial and periaxial, sloping in and up to medial plate, locally replaced by tabulae; stereozone present between tabularium and dissepimentarium if septa dilate in tabularium; corallite wall complete.

*Type species.*—*Ptolemaia ftatateeta*, n. sp.

*Remarks.*—The name *Ptolemaia* is derived from an annual festival celebrated in Hellenistic Alexandria.

*Ptolemaia* may be readily distinguished from *Wentzelella* as revised by Hudson (1958, p. 185) and *Ipciphyllum* Hudson (1958, p. 179) by the number of zones of tabellae. *Wentzelella* and *Ipciphyllum* both have three zones of tabellae—axial tabellae, transverse tabellae, and clinotabellae. *Ptolemaia* has only two zones of tabellae—axial tabellae and transverse tabellae, which may be replaced in places by tabulae (see text-fig. 3). In addition, *Wentzelella* has tertiary




TEXT-FIG. 3—Diagrammatic representation showing structural differences in the tabularia of *Ipciphyllum*, *Ptolemaia*, and *Wentzelella* (as revised by Hudson). Note absence of third zone of tabellae in *Ptolemaia*. D—dissepimentarium; I—axial zone of tabellae, formed of axial tabellae and medial plate; II—periaxial zone of tabellae, formed of transverse tabellae; III—third zone of tabellae, formed of clinotabellae.

septa and commonly has dissepisepta, neither of which is present in *Ptolemaia*.

*Lonsdaleiastrea* Gerth (1921, p. 77) was assigned by Hudson (1958, p. 184) to the Wentzelellinae, although several species (not discussed by Hudson) lack tertiary septa and clinotabellae and thus possibly warrant establishment of a new genus. Hill (1948, p. 133) noted that some of these species from Russia were generically distinct from *Lonsdaleiastrea*. Fomichev (1953, p. 593) erected *Gorskyai* for these species but, as he did not name a type, Hill (1957, p. 51) considered it to be a *nomina nuda*. Some of the species belonging to this group can be distinguished from *Ptolemaia* only by the presence of the discontinuous corallite walls typical of *Lonsdaleiastrea*. *L. cargalensis* Dobrolyubova (1941, *in* Soshkina *et al.*, p. 211,267, pl. LXII, fig. 1) is a particularly good example.

*Ptolemaia* is tentatively assigned to the aulophyllid subfamily Yatsengiinae Hill, which includes only two other genera, *Yatsengia* Huang (1932, p. 31) and *Protowentzelella* Porfiriev (1941, *in* Soshkina *et al.*, p. 179,262). It is readily distinguishable from *Yatsengia* which is fasciculate and has a dibunophylloid (Hill, 1956, p. F291) axial structure.

Fomichev (1953, p. 593) placed *Wentzelella* in synonomy with *Protowentzelella*. We are uncertain, however, to which species of *Wentzelella* he referred, since he listed only two species attributed to Zhizhina for which he cited no reference and for which we have found none. It is therefore possible that the species of Zhizhina could be referred to genera other than *Ptolemaia*. Regardless of this, *Protowentzelella* and *Ptolemaia* are here considered distinct genera.

Porfiriev (1941, *in* Soshkina *et al.*, p. 262) described *Protowentzelella* as

> "cerioid corals, consisting of corallites with well developed continuous external walls. Their internal structure is composed of three concentric zones: external, filled with vesicles and septa; median, filled with tabulae, and central, more primitive than in typical *Wentzelella* and more complex than the columella of *Lithostrotion*."

The type species, *Protowentzelella simplex* Porfiriev (*ibid.*, p. 180,262, pl. XLI, fig. 1) was described as having an axial structure consisting of "median lamella, very seldom of radial lamellae, usually represented by small denticles, and of tabellae developed but locally." In vertical section, a more persistent and complex axial zone of tabellae separates *Ptolemaia* from *Protowentzelella*. Some species of *Ptolemaia* have relatively few axial tabellae in places and may be indistinguishable in vertical section from *Protowentzelella*. In transverse section, however, the two genera are dissimilar. *Ptolemaia* has two or more (usually more) well developed septal lamellae radiating from the medial plate. *Protowentzelella* usually lacks septal lamellae on the medial plate, although one or two short vestigial ones may be present in a few corallites.

The species (all in Soshkina *et al.*, 1941, p. 184–200,262–265, pl. XLII–LIV) formerly assigned to *Wentzelella* and here placed in *Ptolemaia* are *Wentzelella gracilis* Dobrolyubova, *W. intermedia* Porfiriev (raised here to specific rank from *W. timorica* var. *intermedia*), *W. magnifica* Porfiriev, *W.*

*pseudoelegans* Dobrolyubova, *W. pseudoelegans* var. *prismatica* Porfiriev, *W. stylliodophylloides* Dobrolyubova, and *W. stylliodophylloides* var. *radiata* Porfiriev. *Wentzelella* aff. *indica* of Soshkina, Dobrolyubova, and Porfiriev (*ibid.*, p. 184,262, pl. XLII, fig. 1) is here renamed *Ptolemaia uralensis* with the specimen described and figured (*loc. cit.*) designated as type. This is proposed because *Wentzelella indica* has been referred to *Ipciphyllum*.

PTOLEMAIA FTATATEETA, n. sp.
Pl. 123, figs. 1–6

*Description.—External:* Corallum massive and cerioid, hemispheroidal, maximum diameter greater than 20 cm.; calyx deep, walls sloping steeply inward to depth of about 5 mm.; calicular floor horizontal and flat to slightly sagging, with central calicular boss about 2.5 mm. wide, 2.5 mm. high.

*Transverse section:* Corallites 4 to 7 sided, 5 to 10 mm. wide at greatest diameter, generally about 8 mm.; septa of 2 orders, 13 to 17 each, straight to somewhat sinuous, rarely lonsdaleoid; major septa usually withdrawn from axial structure, 1 to 4 mm. long, 0.1 to 0.5 mm. wide, dilate in tabularium, narrowing axially, thin in dissepimentarium; minor septa 0.7 to 1.5 mm. long, confined to dissepimentarium or extending into tabularium a maximum of 0.7 mm., dilate only in tabularium, rarely absent; dissepimentarium width of 2.0 mm. maximum, generally about 1.0 mm. wide; dissepiments concentric, herringbone, pseudoherringbone (rare), or lonsdaleoid (rare); stereozone on axial row of dissepiments separating dissepimentarium from tabularium; axial structure clisiophylloid, formed of thickened medial plate 1 to 2.5 mm. long with 2 to 10 radiating, straight to somewhat sinuous septal lamellae about $\frac{1}{2}$ length of medial plate, and axial tabellae (medial plate without septal lamellae very rare); medial plate rarely continuous with counter (presumed) septum; corallite wall 0.3 to 0.4 mm. wide.

*Longitudinal section:* Dissepimentarium of 1 to 5 (usually 1 to 3) steeply-dipping ranks of large-elongate and small-cystose (less common) dissepiments; tabellae of 2 zones, axial and periaxial; periaxial tabellae flat, gently domed, or slightly sagging, with straight peripheral edges, sloping gently in and up, 15 to 20 per cm.; axial tabellae steeply sloping in and up, fused axially with medial plate, generally about 20 per cm.; tabulae locally present where axial structure weakly developed.

*Documentation.*—Holotype 30267 and paratypes 30268, 30269, 11054, 34599, and 34600 are in the invertebrate type collections of the Museum of Paleontology, University of California, Berkely. Six coralla were available. Preservation is fair to good and a few corallites are fractured. Ten thin sections and numerous polished sections were studied.

*Age and occurrence.*—The specimens were obtained from two localities. The holotype and paratype 11054 are from the University of California Museum of Paleontology, locality B-6199, in the gray limestone beds formlng the uppermost 60 feet of the Ely limestone in the northeast $\frac{1}{4}$ of section 9, Township 13 North, Range 63 East, Ely #3 Quadrangle, Ward Mountain, White Pine County, Nevada. It may be reached by following a well-marked jeep and truck road leading west from the Charcoal Ovens State Park to Martin Spring at the headwaters of Williams Creek and proceeding on foot 0.5 mile due west to the crest of a long ridge. The locality is in the gray limestone beds of the crest, approximately at the point marked by the summit elevation x8512T on the United States Geological Survey 1958 advance sheet (1:24,000) of the Ely #3 Southwest Quadrangle.

Paratypes 30268, 30269, 34599, and 34600 are from the University of California Museum of Paleontology locality B-6162 in a gray limestone bed 32 stratigraphic feet below the top of the Bird Springs formation in the southeast $\frac{1}{4}$ of Township 14 South, Range 64 East, Arrow Canyon Quadrangle, Arrow Canyon Mountains, Clark County, Nevada. It may be reached by following U. S. Highway 93 northwest from Glendale Junction for 12 miles and proceeding west along a side road for $2\frac{1}{4}$ miles into Arrow Canyon. The locality is on the west face of a subsidiary spur on the north wall of the canyon, at approximately 2560 feet elevation and 32 stratigraphic feet below the ledge capping the spur. It may be located on

the U. S. G. S. Arrow Canyon Quadrangle (1:62,500) 1958 at about 0.1 mile west of the center of the western edge of section 7, Range 65 East, Township 14 South.

Age assignment at both localities is based upon Wolfcampain fusulinid faunas.

*Discussion.*—Axial structures of the holotype and paratypes are somewhat different. In the former, septal lamellae are generally fewer and axial tabellae between the septal lamellae (as seen in transverse section) tend to be straight and their junction angular, whereas the latter generally have more septal lamellae and the axial tabellae are somewhat sinuous with rounded junctures, giving a cystose appearance to the axial complex. We feel that these differences are not of specific significance as the specimens are essentially identical in all other features.

The other species and varieties assigned to *Ptolemaia* are all from the Lower Permian (Sakmarian and Artinskian) of the Ural Mountains. They may be distinguished from the type species by the following differences. *P. stylidophylloides* has extremely thin structural elements, poorly developed to absent minor septa, a loosely defined axial structure, and highly inflated dissepiments which occur in only 1 or 2 ranks. *P. stylidophylloides* var. *radiata* differs similarly, except that it does not have inflated dissepiments. *P. magnifica* has somewhat more septa (15 to 22), minor septa that are often absent, and a more irregular axial structure. *P. intermedia* has septa which are commonly fused with the axial structure and axial tabellae which are less steeply inclined. *P. uralensis* has undilated major septa, longer minor septa, and an irregular axial structure. *P. grandis* has shorter minor septa (often lacking) and a wider, locally lonsdaleoid dissepimentarium. *P. gracilis* is very similar, but many major septa commonly reach the axial structure, in which stereoplasm is commonly present. *P. pseudoelegans* is similar in all features except that the septa are not dilate. *P. pseudoelegans* var. *prismatica* also has undilated septa and more major septa (as many as 22).

*Lonsdaleia illipahensis* Easton (1960, p. 580, text-fig. 15,16), also from the Permian of Nevada, is similar to *Ptolemaia ftatateeta* in general appearance, but may be distinguished by the following characters. The dissepimentarium of *Lonsdaleia illipahensis*, although not wholly lonsdaleoid, appears to be predominately so, whereas the dissepimentarium of *Ptolemaia ftatateeta* is regular, with rare lonsdaleoid septa. In *Lonsdaleia illipahensis* the major septa are usually in contact with the large axial structure, while *Ptolemaia ftatateeta* has a smaller axial complex and predominately withdrawn septa. Otherwise, the two species are notably similar in septal number, corallite diameter, ranks of dissepiments, zones of tabellae, and other features. However, even if *Lonsdaleia illipahensis* should prove referable to *Ptolemaia*, the differences in size of the axial structure and its relation to the major septa should be considered specific for reasons presented by Gorsky (1952, p. 52), who states:

> "The use of the narrow interpretation of species, especially in view of the homomorphism which is rather frequent among corals, implies a possibly complete knowledge of the ontogeny of each species with a series of slides. This will not only enable the morphologic peculiarities and their development in the given form to be deciphered, but also the genetic relations to be understood between allied forms, even though close relations between them are not always morphologically evident at different stages of development."

An undescribed new species of *Syringopora* occurs with *Ptolemaia ftatateeta*. Since both species are seemingly lacking elsewhere in Permian sections which were studied at Ward Mountain, White Pine County, Nevada (Wilson, 1960) and at Arrow Canyon, Clark County, Nevada (McCutcheon, 1961), their restricted association suggests a correlation between the two localities.

*Conclusions.*—*Ptolemaia* is assigned to the Aulophyllidae because of its similarity to the other genera of the Yatsengiinae, a subfamily which Hill (1956, p. F291) referred to the Aulophyllidae. This subfamily lacks the fossula which largely characterizes the Aulophyllidae. The Yatsengiinae seem closely allied to the Waagenophyllidae, differing mainly in the elements of the tabularium, which consists of three zones of tabellae in the latter and only two zones in the former. The Yatsengiinae also might be

referred to the Lithostrotionidae as the subfamily with the most complex axial structure. Two genera of the Lithostrotionidae, *Nemistium* Smith and *Tschussovskenia* Dobrolyubova both have somewhat complex axial structures. We feel that no family of the Rugosa, as they are currently restricted, can satisfactorily accommodate the Yatsengiinae. Perhaps this subfamily should form the basis for a new family or be included in a revised version of one of the above families.

Inasmuch as the relationships of Permian colonial corals are imperfectly understood, we feel it desirable, for stratigraphic utility as well as taxonomic clarity, to split taxons on a refined basis. This necessitates more adequate descriptions and illustrations than has been previously customary with many investigators.

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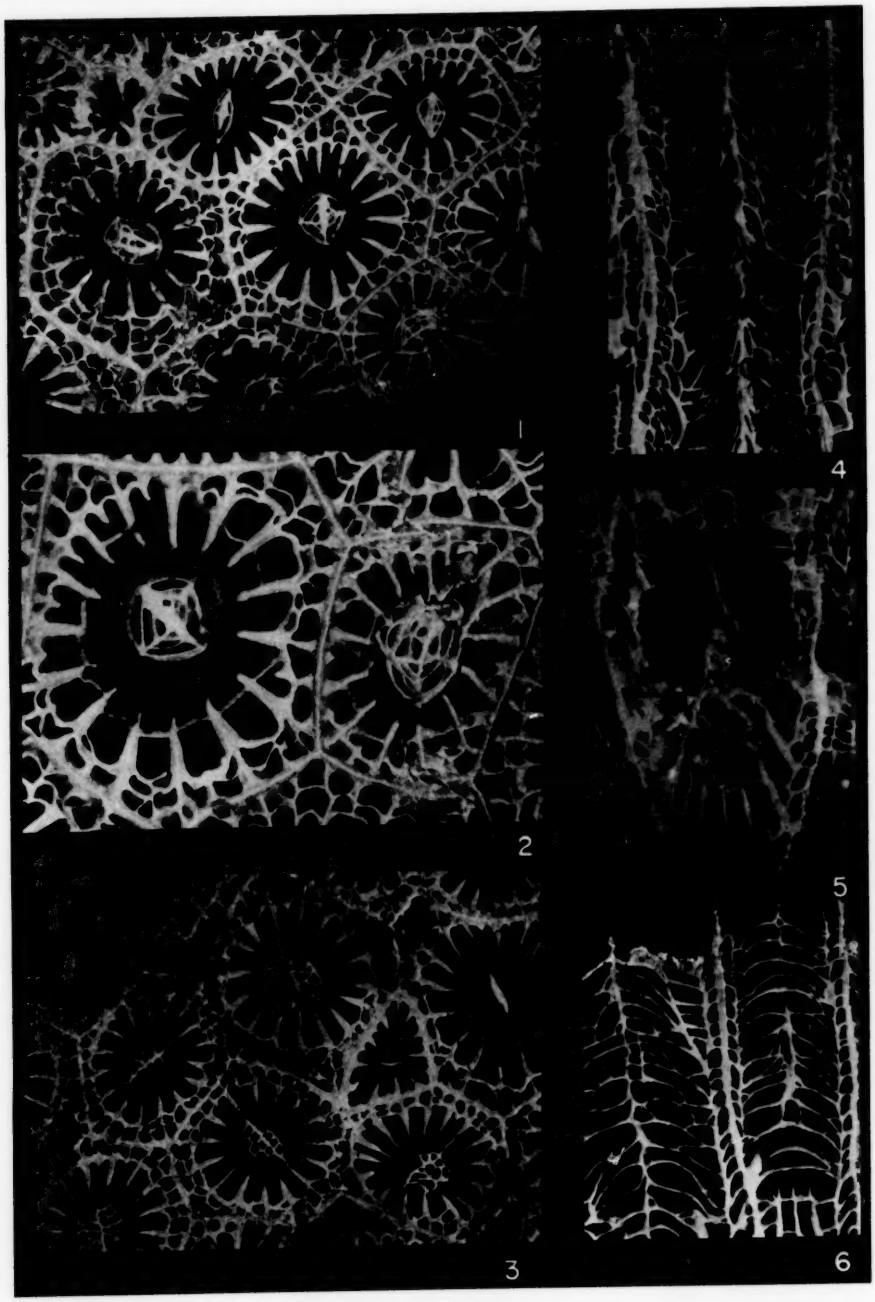
MANUSCRIPT RECEIVED SEPTEMBER 25, 1960

EXPLANATION OF PLATE 123

(All photographs slightly retouched; traces of periaxial tabellae inked out for clarity in figs. *1* and *3*.)

FIGS. *1–6*—*Ptolemaia ftatateeta*, sp. nov., *1*, transverse section of holotype UCMP 30267, ×4.5; *2*, transverse section of holotype UCMP 30267, ×8.5; *3*, transverse section of paratype UCMP 30268, note mature corallite with axial structure of medial plate only, ×4.5; *4*, longitudinal section of holotype UCMP 30267 showing two zones of tabellae, ×4.5; *5*, oblique longitudinal section of paratype UCMP 30268, ×5; *6*, oblique longitudinal section of paratype UCMP 30268 showing immature corallite with tabulae as well as tabellae, ×5.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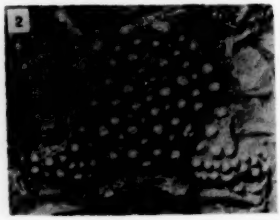
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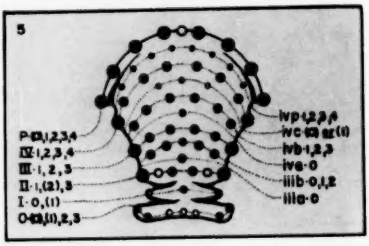

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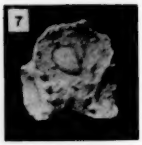
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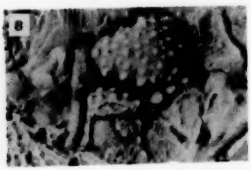
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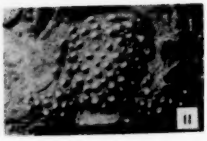
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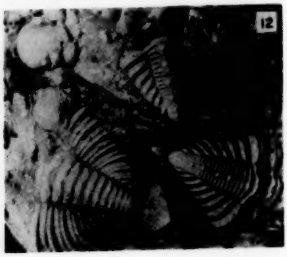
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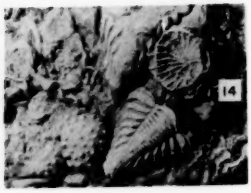
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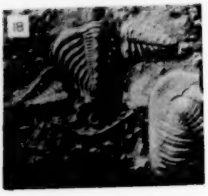
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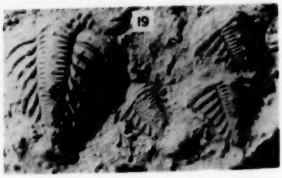
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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1029–1040, PL. 124, 1 TEXT-FIG., SEPTEMBER, 1961

# INTRASPECIFIC VARIATION IN *ENCRINURUS ORNATUS*

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ABSTRACT—A local population of *E. ornatus*, represented by samples of 450 pygidia from shales and 450 from the carbonate interbeds, in a 1¼-foot interval in the upper Lockport at Hamilton, Ont., is described: details include glabellar formula based on 25 cranidia.

The first three axial tubercles of the pygidium occur at intervals of 4 rings or 3. The numbers of pygidia, with intervals from the first to third tubercles of 8, 7 and 6 rings respectively, closely approximate a binomial in each sample of 450, but the frequencies of different types of tubercle spacing differ significantly between carbonates and shales: tubercles tend to be more closely spaced in the carbonates.

The facts are interpreted as evidence of:

1. Operation of the Hardy-Weinberg law of genetics: the random distribution of genetically-controlled features indicates that these trilobites were either actually or potentially interbreeding: a corollory is that, although dimorphism has not been recognized, reproduction was necessarily sexual;
2. the conditioning influence of environment: the closer spacing of tubercles in carbonates suggests that they were neither tactile nor luminous but light-controlled, probably light-sensitive organs.

## INTRODUCTION

OVER the last three years the writer has obtained nearly a thousand pygidia and more than a hundred cranidia of *Encrinurus ornatus* Hall and Whitfield from a stratigraphic interval of at most one and a half feet, in the Eramosa member of the Lockport formation (Mid Silurian) above Dundas, Ontario. Such a large sample from so small an interval provides unusually good material for study of intraspecific variation.

The first few specimens collected from Dundas displayed such a range of variation that the question arose whether more than one species were represented. The original intention in obtaining more was merely to have a big enough sample to settle the first question and, if it were only a single species, to establish its degree of variability.

As collecting techniques improved and

## EXPLANATION OF PLATE 124

*Encrinurus ornatus* Hall and Whitfield

(Figs. 1–3,6,8,10,13, ×2.5; all other photographs ×1.5)

All figured specimens McMaster University, Cat. nos., respectively, of figs. 1–4, S 336-S 339: of figs. 6–20, S 340-S 354.

FIGS. *1–4,6–8,11*—Cranidia: *1–3,4,11*, showing distribution of tubercles and variable number in front row (note composite lateral tubercles on flattened glabella of Fig. *2*); *6*, lighted from upper right to show tuberculation of eye-stalk and lateral tubercle of preoccipital lobe; *7,8*, ventral and lateral views showing how inter-tubercle identations and marginal furrow correspond with internal apodemes.

*5*—Glabellar formula generalized from 25 complete glabellae; tubercle positions occupied in 18 or more, blacked in: those not blacked in (given in parentheses), occupied in 10 to 15: positions occupied in fewer than 6 are not shown.

*9*—Hypostome.

*10*—Right free cheek showing tubercles with granular ornament preserved and eye-stalk with smooth, terminal visual area.

*12,14*—Portions of slabs: *12*, with two pygidia: note also *Dizygopleura* (top right), glabella of *Calymene* (top left) and pygidium of *Dalmanites* (bottom left); *14*, with two complete pygidia (the smallest, at top, 2 mm. long) and a cranidium.

*13,15–20*—Pygidia: first axial tubercle of *13,17* on first ring; of *18* (the centre one), *20* on third ring; of all others on second ring; *16* shows 9 ribs (8 complete to margin); *19* illustrates the four alternative modes of spacing of first three tubercles.

the size of the sample grew it became apparent that only one species was present, but the objectives were enlarged to include some data on the influence of differing environments on parts of what seemed to be a single, local population.

A lot more remains to be done, particularly on the paleoecology and specific assignment of the associated fossils, but the data accumulated so far reveal such interesting intraspecific relationships that it seems worth bringing to the attention of others: the principles involved should be applicable to almost any well-represented fossil species.

The numbers of pygidia in three groups, of which two are end members of a continuous morphological series, and the third intermediates, in a stratigraphically limited sample, very closely approximate a binomial. This distribution seems to be best interpreted, by reference to the Hardy-Weinberg law of genetics, as evidence of genotypic equilibrium in a single, either actually or potentially interbreeding population. This collection of *Encrinurus* then, represents a species in both the paleontological sense and the neontological.

Within the same stratigraphic interval, although all types of pygidia present in carbonates also occur in shales, the frequencies of the features which are distributed binomially differ significantly between the two lithologies. This certainly indicates response to environment and suggests the operation of selection pressure.

ACKNOWLEDGMENTS

Jon Weber and Arne Brackenridge of McMaster University undertook the study of the first 100 pygidia, George Vinc of the first dozen cranidia: these and many others helped materially in collecting.

Special thanks are due to Dr. W. R. Evitt and Dr. H. B. Whittington for encouragement to undertake the study, for fruitful discussion and loan of important references, and to Drs. E. Mayr, H. B. Whitting and A. B. Palmer for critical comments on the manuscript.

The project would have been impossible without research grants provided by McMaster University.

FOSSIL LOCATION AND ENVIRONMENT

The fossils were collected from the floor of the old part of the Canada Crushed Stone quarry, about 300 feet north of the dumping chute. The beds sampled, between 34 and 36 feet below the base of the Guelph dolomite, are part of a 10 foot sequence of thin carbonates and shales and consist of two 3–6 inch, dark brown, bituminous, calcareous shales separated by a single 0–4 inch bed (it lenses out into the shale) of calcareous bioclastic dolomite. The whole dips gently (about 1–1½ degrees) southwest.

The fossils, although partly dolomitized and, in the shales, somewhat distorted by compaction, are very well preserved. The associated fauna is too prolific in genera and species to be discussed completely (it also requires further study) but a few observations are worthy of record.

The only trilobites found in these beds are *Encrinurus*, *Calymene*, *Dalmanites* and *Acanthopyge*, in order of abundance respectively 100:10:2:1 (the last has only been seen in the carbonates). Both in systematic position and relative abundance these contrast markedly with those observed by Lowenstam (1957, p. 239) in the reefoidal deposits of the Great Lakes area further south, where *Sphaerexochus* and *Encrinurus* are characteristic of the initial, quiet water stage of reef growth and *Bumastus* and *Calymene* of the late, rough water stage.

Bolton and Liberty (1955, p. 29–34) indicate that the Eramosa beds were deposited in an inter-reef or pre-reef environment. The Guelph dolomite is certainly reefoidal but it is not known whether reefs contemporaneous with the Lockport grew eastward of the present escarpment; at any rate a similar trilobite fauna to that reported by Lowestam is to be expected, but neither *Bumastus* nor *Sphaerexochus* is represented in the collection.

All forms of *Encrinurus* pygidia so far recognized, and *Dalmanites* and *Calymene*, are found in both carbonates and shales. In the shales ostracodes are common (*Kloedenella*, *Dizygopleura*, *Aechmina*, *Paraechmina*, *Primitia* and a few *Beyrichia*); *Favosites* is found in growing position; brachiopods include *Whitfieldella* (juvenile),

*Stegerhynchus* and *Leptaena* (about 5:5:3); bryozoa are represented by *Nematopora* and *Fenestella*, worms by *Cornulites* and *Spirorbis*. *Tentaculites* (whether worm or gastropod?) is common also. In the carbonates (on the top surface of the carbonate bed underlying the sampled shales and of the interbed) the ostracodes do not appear to be so abundant; *Favosites* is not always in growing position and solitary rugose corals (uncommon in the shales) are fairly numerous; the brachiopods include *Stegerhynchus*, *Reticularia* and *Leptaena* (about 5:5:2) and a few *Craniops* (generally parallel to the surface: probably in growing position); *Whitfieldella* is rare here but completely covers the surface of carbonate beds only 2 feet above this. Both bryozoa and worms (and *Tentaculites*) appear to be less common in the carbonates than in the shales; coiled gastropods are equally represented in both rock types.

In both carbonates and shales crinoidal debris is important quantitatively but in the former there seems to be a higher percentage of disarticulated brachiopods and broken trilobite parts (pl. 124, fig. 12).

The mineralogical composition of some of the fossils requires further study. Many are unusually rich in iron, generally as hematite, but the replacement appears to be systematically selective. *Encrinurus*, *Dalmanites* and *Acanthopyge* are nearly invariably red, but less than 20% of the associated *Calymene* specimens are similarly stained. More than 40% of *Kloedenella* and *Dizygopleura* are stained red (or dark green) but not *Primitia* (and complete ontogenies from 0.3 to more than 1 mm. of all three are represented). Among the brachiopods *Leptaena* alone is nearly always red: all the others are of the same color as the host rock. Similarly, *Tentaculites* is always red or green but *Cornulites* seldom and *Spirorbis* never. None of the coiled gastropods is red or green, but about 60% of them are dark grey.

These color contrasts hold good in both carbonates and shales and, on the same bedding plane, specimens of the same species may be colored red (or dark green) or the usual grey-brown: there is no systematic evidence that any are derived fossils. Similarly, apart from the possibly increased number of disarticulated brachiopods in the carbonates, there is little physical evidence of reworking: indeed, preservation of very fine granular ornament on delicate, freshly exposed trilobite remains suggests that if reworking did obtain at all, it must have been a very gentle process, occurring while the sediments were still entirely unconsolidated.

The association of the fossils mentioned above in alternating thin layers of bioclastic carbonates and shales, occasionally broken (but rarely abraded) in the carbonate lenses, indicates fluctuations in supply of detrital clays, or in turbulence of water, or both; there is no hint of preferred orientation to suggest current action. No stromatoporoids are present and only a few cryptostome bryozoa: the only calcareous algae seen are of the jointed, dendritic type (? *Corallium*): thus, practically no organisms capable of serving a reef-cementing funtcion are present. The water was probably not more than 20 or 30 fathoms deep in an inter-reef or pre-reef area, below wave base during deposition of the shales and only slightly above while the carbonates developed.

### SAMPLING AND PREPARATION

The locality sampled measures about 150 feet across, with the stratification nearly coincident with the quarry floor. The fossils from the shales are naturally weathered and lying loose (but admittedly a few from the carbonates may be included). Those tightly adhering to or embedded in carbonate slabs are taken to be characteristic of that environment. Several large slabs up to 3 feet across were removed and covered with NaOH pellets for three days to loosen adherent shale.

When the first 250 pygidia were examined initially no attempt was made to distinguish between fossils from shales and those from carbonates. Later, these were separated into unequivocal carbonate (89) and inferred shale material (161). The additional pygidia were collected personally from known lithology and, to the best of my knowledge, no specimens from above or below the 1½ foot interval were used in the final analysis. As a final check, three other sections in the same quarry were examined

and correlated: there too, the encrinurids are concentrated mainly in a 1- to 2-foot interval.

METHOD OF STUDY

In selecting the first 250 pygidia the main criteria were completeness of at least 18 axial rings and possession of rib tubercles from the first to the fifth rib. In the specimens added later and in all used for table I attention was focussed on the anterior portion of the pygidium, particularly the axis.

As a rule, axial tubercles occur no more frequently than on every third or fourth ring but, in about 5% of specimens, the normal large tubercle may be augmented by one on an adjacent ring (pl. 124, fig. 14). In a few specimens two or more tubercles occur clustered on a single ring: in this case only one tubercle was recorded. Thus, in preparing text-fig. 1, all occupied rings were recorded by number. In analyzing spacing, however, (table I) the matter of which ring-number is occupied becomes important: where a large tubercle of the first three and a small one occupy adjacent rings only the larger was recorded but, if the two are of equal size the ring-interval is indeterminate and the specimen had to be discarded (only six were eliminated for this reason).

Five specimens lack a tubercle in what might be regarded as a 'normal' position (e.g., occupied rings were 2,10,14, etc.); four have an extra one (e.g.,: 2,4,6,10, etc.). These also were disregarded in preparing table I.

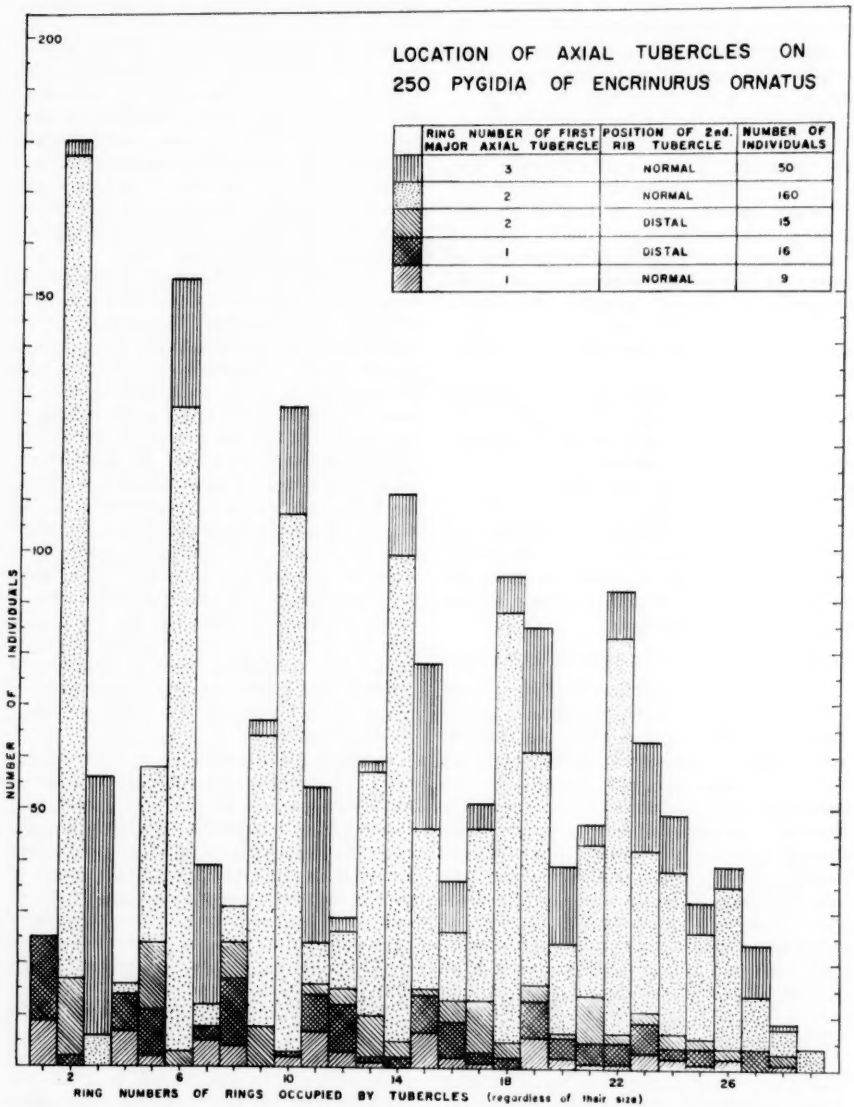
Asymmetry in the axis or pleura was observed in at least 5% of specimens. In recording tubercle positions for text-fig. 1, where more rings could be counted on one side of the axis than on the other, the larger ring number was used. However, where the partial ring occurs within the first 11 complete ones the specimens (only two) were omitted in preparing table I.

Several factors are responsible for the decrease in regularity of tubercle spacing shown in text-fig. 1.

First, as noted below there is a definite reduction ln regularity of spacing towards the rear. Second, the smaller the pygidium the fewer are the observable rings (e.g.: the specimen, 2 mm. long, of pl. 124, fig. 14 has no more than 20 rings and 5 tubercles): even on some of the larger ones there are no tubercles beyond the 22nd ring: accordingly,

TABLE I—SPACING OF FIRST THREE AXIAL TUBERCLES IN 900 PYGIDIA OF *E. ornatus*

| Rock type | Ring intervals 1st 3 tubercles | First tubercle on ring number 1 | 2 | 3 | Σ |
|---|---|---|---|---|---|
| Carbonates | 4, 4 | 7 | 139 | 31 | 177 |
| | 4, 3 and 3, 4 | 39 | 150 | 25 | 214 |
| | 3, 3 | 12 | 40 | 7 | 59 |
| | Σ | 58 | 329 | 63 | 450 |
| Shales | 4, 4 | 5 | 172 | 45 | 222 |
| | 4, 3 and 3, 4 | 21 | 131 | 39 | 191 |
| | 3, 3 | 12 | 20 | 5 | 37 |
| | Σ | 38 | 323 | 89 | 450 |
| Total | 4, 4 | 12 | 311 | 76 | 399 |
| | 4, 3 and 3, 4 | 60 | 281 | 64 | 405 |
| | 3, 3 | 24 | 60 | 12 | 96 |
| | Σ | 96 | 652 | 152 | 900 |




TEXT-FIG. *1*—Histograms illustrating the tendency for tubercles to occur on every fourth ring and the reduction in regularity towards the rear in 250 pygidia of *Encrinurus ornatus*.

there is an actual decrease in number of tubercles towards the right hand side of the histogram. Finally, it is difficult, even on well-preserved material, to assign posterior tubercles to particular rings and to recognize every instance of axial asymmetry.

As indicated by Whittington (1957, p. 442) holaspids of some trilobite genera may have continued to proliferate at the posterior extremity of the axis. If *Encrinurus* did, some correlation may be possible between irregularity of tubercle distribution and the stages (and even environment) in which the respective rings and tubercles developed, however, no attempt was made to relate spacing of posterior tubercles with environment.

Whatever the reason for its rearward decrease in regularity, the tendency to tetrad arrangement of tubercles on specific rings suggests merocyclism (a term introduced by Raw (1953) for periodicity of a macrosomite alternating cyclically with one or more normal segments in annelids and trilobites). If, as suggested below, the tubercles were light-sensitive organs, it raises the question whether all merocyclism has an original sensory function.

### SPACING OF THE FIRST THREE TUBERCLES

Axial tubercles most commonly occur on every fourth ring of the pygidium (regardless of whether the first one is on the 1st, 2nd or 3rd ring): anteriorly the interval may be three rings, whereas posteriorly the regularity of spacing tends to decrease (text-fig. 1), and the interval may range from 3 to 5 or more. In more than 98% of pygidia (from 2 mm. to 17 mm. long: the rule holds regardless of size) the first three major tubercles are situated at intervals of either four or three rings, or both: that is, on specimens in which the first tubercle is on #2 ring the possibilities are: 2, 6, 10 or 2, 6, 9 or 2, 5, 9 or 2, 5, 8 (pl. 124, fig. 19): thus the intervals may be *4,4, 4,3 or 3,4, 3,3.*

In the first 250 specimens it was noticed that these three types of tubercle spacing were represented respectively by 122(?), 104 and 24 individuals. Regarding 4-spacing and 3-spacing as opposing tendencies it was difficult to avoid the conclusion that 4,3 and 3,4 might represent hybrids of 4,4 and 3,3 parents, or, more likely, that the two tendencies represent the operation of a pair (or several pairs) or alleles.

If a population is either actually or potentially in equilibrium (interbreeding) with respect to a particular feature, controlled either by a single allelic pair or by several pairs having their common morphological expression in this one feature, the numerical proportion of 'end-members' and intermediates to each other should be in accordance with the well-known Hardy-Weinberg law of genetics (Srb and Owen, 1958).

If the frequencies of two alternative genes or genetic tendencies are termed a and b, in a freely interbreeding population of N individuals the numbers in the three groups should form a binomial of the form $(N)(a^2+2ab+b^2)$. It is as if two dice were marked only with 4's and 3's: 4's on four of the faces and 3's on the other two. (The frequencies here would be .67 and .33 respectively.) Over a large number of trials, say 900, the expected numbers of 8's, 7's and 6's rolled should approximate a binomial: two 4's should occur 400 times, a 3 and a 4 together 400 times and two 3's 100 times. In other words, what we are looking for is randomness. Since tubercles on the pygidium of *Encrinurus* were almost certainly genetically controlled, proven randonmess of their distribution in the sample may be taken as evidence of at least potential interbreedability.

It might be argued that, in a sample of only 250 pygidia, the approach to a binominal in spacing of the first three axial tubercles ls accidental. If, however, the respective categories significantly change in proportions between two unlike environments but maintain the binomial form in two much larger samples, it is so improbable that such a situation could arise by chance that at least potential interbreedability may be regarded as "proven."

With this thought in mind another 750 pygidia were collected, keeping the carbonate specimens separate from those from shales. (It was hoped to raise the total to 1000 but the supply of shale specimens, hardest to obtain, ran out at 450.) Five specimens were discarded from the first 250 for reasons noted above and the two collections were added to, strictly as they came, until data on 450 usable speci-

mens of each had been obtained. The data for the final 900 are given in table I.

The figures given in table I are highly suggestive.

In the carbonates for example, the frequency of the 4-spacing and 3-spacing and the expected numerical distribution (assuming a binomial) may be arrived at simply:

| *Actual No's.* | *No. of 4's & 3's* | *Frequency* | *Expected No's.(e)* |
|---|---|---|---|
| 177 | $2(177)+214=568$ | $\frac{568}{900}=.63\dot{1}$ | $(.63\dot{1})^2 450=179.23\dot{5}$ |
| 214 | | | $2(.63\dot{1})(.36\dot{8})(450)=209.52\dot{8}$ |
| 59 | $2(59)+214=568$ | $\frac{332}{900}=.36\dot{8}$ | $(.36\dot{8})^2 450=61.23\dot{5}$ |
| $N=450$ | | | |

The closeness of fit may be tested by $\chi^2$ test:

| Differences | (d) | $d^2$ | $\frac{d^2}{e}$ | |
|---|---|---|---|---|
| | $2.23\dot{5}$ | 4.9977 | .0271 | $\chi^2=\Sigma\frac{d^2}{e}=.204$ |
| | $4.47\dot{1}$ | 19.9908 | .0955 | |
| | $2.23\dot{5}$ | 4.9977 | .0819 | |

of the sum (or mean), it may be shown by $\chi^2$ test that the distribution

Entering tables of $\chi^2$ with one degree of freedom, a value of .204 corresponds to a p value of about .65. If numerous similar samples were taken from a population in which the Hardy-Weinberg law operated with these gene-frequencies, 65% of the samples could be expected to show no better approximation to the binomial than this.

Similarly, in the shales respective frequencies are .705 and .294 and the calculated or expected values are, respectively, 224.014, 186.972, 39.014 (where actual values are 222, 191, 37). Again $\chi^2$ is low (.209) and p fairly high (.64).

The following points are worthy of note:

(a) The distribution of 4-spacing and 3-spacing in carbonates and shales each independently approximates a binomial. It is therefore considered very likely that each represents a single population, either actually or (more probably) potentially freely and randomly interbreeding. A corollary to this is that reproduction would of necessity be sexual rather than asexual.

(b) Taking either one of the two differing samples as standard and testing the distribution of the other against it, or testing both against the distribution of 4-spacing to 3-spacing in the carbonate sample differs significantly from that in the shale: the spacing of pygidial tubercles in the carbonates appears to be *closer* than it is in shales.

(c) An independent check is provided by the relative percentages, between carbonate and shale, of pygidia in which the first axial tubercle occurs on the first ring and those in which it occurs on the third ring. The second thoracic spine in this species of *Encrinurus* is located on the tenth thoracic segment. One thoracic segment intervenes before the first pygidial ring. The interval, therefore, from the last thoracic spine to the first pygidial tubercle may be 2, 3 or 4 rings. The proportion of specimens with the first tubercle on the first ring is higher in carbonates than it is in shales, al-

though the number with the first tubercle on the second ring remains about the same. This again suggests that spacing tends to be closer in carbonates than shales.

(d) In each sample of 450 the numbers of specimens in the first column (first tubercle on first ring) and in the last row (3,3 spacing of first three tubercles) is practically the same, but no explanation has presented itself so far: other genes, of unknown potential, may have been at work.

(e) The close approximation of the total to a 4:4:1 binominal (i.e. 399:405:96) is inevitable where the respective frequencies of the two halves (each of which is binomially distributed) differ by as little as between .706 and .631. By the same token it must be admitted as possible that the shale sample of 450 may itself represent the sum of two or more subpopulations with only slightly varying gene-frequencies. The carbonate material, however, appears to be reliable: 228 specimens on a single bedding plane within an area of 10 square feet give figures of 92, 106, 30 for the 4,4:4,3 and 3,4:3,3 tubercle spacing and 32, 166, 30 for those with the first tubercle on the 1st, 2nd and 3rd rings respectively: proportionately, a very close approximation to the whole sample of 450.

It is evident that axial tubercles in the pygidium of *Encrinurus ornatus* tend to be more closely spaced in carbonates than in shales. But explaining the fact is not so easy. In their original condition the tubercles appear to have been imperforate externally, but the slightest abrasion reveals one or more canals opening inward to the ventral surface of the integument. Retention of tubercles in successive species over many millions of years suggests that they must have been adaptive—*Encrinurus* ranges from the Mid Ordovician to late Mid Silurian—but what was their function?

In proposing a function for the perforated tubercles of trilobites, Harrington, following Whittington and Evitt (1954) and others, favors "passageways for tactile setae" or possible "external openings of cutaneous or subcutaneous glands" (Harrington, 1959, p. O94). On the other hand, Kummerov (quoted by Brooks, 1957, p. 991) interpreted the tubercles of *Encrinurus* as luminous organs.

It is difficult to see how tactile organs would be affected by the differences in bottom conditions which result in depositional changes from limestone to shale or vice versa, but light does vary with depth and the amount of suspended clastics: it is therefore more plausible that tubercles would have had a function in which light plays an important part. But luminosity is unlikely: the evidence suggests a greater need for tubercles in the shallower or cleraer water carbonate environment than in the deeper or darker water where the shales were deposited.

Of course, it is not necessarily true that bioclastic carbonates, developed only periodically by invasions of the depositional locus by wave base, represent clearer water than shales deposited below wave base. However, taking all the available facts into consideration, the most likely explanation seems to be that these tubercles of *Encrinurus* represent light-sensitive organs, possibly related in some way to the necessity for camouflage.

It is concluded that the discovery of binomial distribution with respect to a single feature (in its essence the Hardy-Weinberg relationship of genetics), in a fossil species, is a useful check on purely geological observations. In this instance it seems to constitute evidence of genotypic equilibrium in a single population. At the same time, relating minute morphological differences to changes in environment seems to provide evidence of selection pressure. Furthermore, the old problem of equating the paleontological concept of species with the neontological—the matter of interbreedability can apparently be solved by the use of large enough samples. Finally, apart from purely practical considerations, it is pleasing to be able to make randomness work for us rather than against us: one is reminded of the dictum from another discipline: "If you can't beat them, join them."

SYSTEMATIC DESCRIPTION

*Encrinurus ornatus* Hall and Whitfield, 1875
Pl. 124, figs. 1–20

*Cybele punctata*, Hall (1852) Pal: New York, v. 2, p. 297; Pl. 66A, fig. 1.
*Encrinurus ornatus*, Hall and Whitfield (1875) Pal. of Ohio, v. 2, p. 154; pl. 6, fig. 16.
*Encrinurus thresheri*, Foerste (1887) Bull. Sci. Lab. Denison Univ. v. 2, p. 101; pl. 8, fig. 26.
*Encrinurus ornatus*, Norton (1896) Proc. Iowa Acad. Sci., v. 3, p. 79–81. (possibly distinct:—see p. 24)
*Encrinurus punctatus* (part) and *E. ornatus*, Vogdes (1907) Trans. San Diego Soc. Nat. Hist., v. 1, No. 2, p. 68–69; Pl. I, fig. 5; Pl. 3, figs. 15,15A.
*Encrinurus ornatus* and *E. thresheri*, Raymond (1916) Bull. Mus. Comp. Zool., v. 60, no. 1, p. 26.
*Encrinurus cf. ornatus*, Foerste (1919) Ohio Jour. Sci., v. 19, no. 7, p. 391; pl. 18, figs. 2a,b.
*Encrinurus ornatus*, *E. thresheri* and *E. hillsboroensis*, Foerste (1919–24) Bull. Sci. Lab. Denison Univ., v. 19, p. 79–80; pl. 18, figs. 9a,b,10.
*Encrinurus ornatus*, Walter (1924?) Geol. Surv. Iowa, v. 31, p. 272–275; pl. 23, figs. 11–15.
*Encrinurus ornatus*, Swartz and Prouty (1923) Geol. Surv. Maryland, Silurian, p. 705; pl. 33, figs. 9,10.

The following description is based entirely on material from the Eramosa member, Lockport Formation, at Dundas, Ontario

Cranidium is tuberculate: tubercles of various sizes appear at first glance to be crowded irregularly over the glabella and cheeks. The tubercles are usually conical on small individuals and wart-shaped on large. The whole dorsal surface, including that of tubercles, is granular, but on weathered or abraded specimens the granulation is missing at the apex and each tubercle is seen to have a cental perforation enlarging downward. The lateral glabellar tubercles in a few cranidia are composite, each seeming to consist of two or three haphazardly superimposed (pl. 124, fig. 2), but whether these tubercles are single or composite the perforations appear to be normal to the plane of the cephalon, not to the lateral glabellar surface. The perforations of the anterior border tubercles, however, do open normal to the glabellar surface.

Internal views of the glabella (pl. 124, fig. 7) show that five inwardly-projecting apodemes correspond to inter-segmental divisions which are marked dorsally only by slight indentations between the tubercles of the lateral row. The smallest apodemes (the anterior pair) correspond to the only distinct furrow on the dorsal side (the marginal furrow).

The occipital ring is equipped with a pair of small antero-lateral tubercles and usually a fairly large pair of lateral ones just inward from and behind them (pl. 124, fig. 1): further in there may be a smaller, second pair on the posterior margin (pl. 124, fig. 11) and, less commonly, a central tubercle: (for all tubercles except the row immediately behind the marginal furrow, notation follows that used by Tripp 1957, p. 61).

The preoccipital segment is small and, in nearly all cranidia, has a medium sized central tubercle (pl. 124, figs. 1,2,4,8,11,14). In about a quarter of the specimens showing the preoccipital lateral lobes the tips are marked by a pair of minute tubercles (pl. 124, figs. 4,6).

The anterior four of the six observable cephalic segments are terminated distally by a row of large lateral tubercles, the anterior pair separated from the other three by incomplete marginal furrows (pl. 124, figs. 3,6).

The central tubercles were examined on 25 complete glabellae and a summary of their distribution is given in the diagram of pl. 124, fig. 5. It should be stressed, however, that no glabella studied so far conforms exactly to the glabellar formula: each has individual peculiarities. Tubercles regarded as typical may be small, or slightly displaced, or doubled: extra ones may appear anywhere except in the lateral rows.

Although tuberculation of the cranidium is very variable, examination of more than 100 (25 with complete glabellae) disclosed no morphological features which could be used to segregate cephala into three groups corresponding to pygidia in which the first tubercle occurs on the 1st, 2nd or 3rd axial ring, or into two distinct lithological groups, from carbonates and shales.

One difficulty arose in preparing the glabellar formula: by convention intermediate rows are given the number (lower case) of the next row in front (ibid). How-

ever, the row of minor tubercles anterior to row IV terminates on either side behind the marginal furrow, but does *not* appear to represent another segment. As this row is clearly not preglabellar it would be incorrect to label it p and it can hardly be labelled iv without qualification. As a compromise it is given as ivp (pl. 124, fig. 5).

The front row of tubercles (p) corresponds to the anterior border: it consists basically of 8 tubercles but small ones may be interpolated in spaces between the large, most commonly in the central space. Whether a central tubercle is present or not, the anterior margins of the cranidium, bounded by sutures, meet at an angle of about 140 degrees.

The inner edge of the fixed cheek has a row of fairly large tubercles which alternate with the lateral ones of the glabella, but those of the posterior limb are irregularly distributed; the genal spines generally have three at their bases.

The eyes are pedunculate, constricted near the base of the stalk. The fixed cheek half of the stalk possesses a row of four tubercles halfway up (pl. 124, fig. 6) and is finely tuberculate and granular from there to the tip; the free cheek half, devoid of tubercles, is granular to halfway up and then smooth to the tip: individual lenses have not been seen on the terminal portion.

The rostrum has not been recognized. (The angular anterior margin of both cranidium and hypostome suggests that there may not be one.)

The hypostome (pl. 124, fig. 9), large relative to the size of cephalon, is robust and almost as commonly preserved as the pygidium. It is easily recognized by its blunt, nose-like anterior termination which extends back as a low mound onto the median body. The anterior border is gently curled downward and extended into a triangular point of about 115 degrees. The border furrow, marking the deepest portion of the lateral notch, leads into the anterior wing pit. The median body is oval, with two pronounced, posterolateral maculae. The posterior border is entire and extended to form a bluntly subtriangular blade, the sides forming an angle of about 60 degrees. The outer surface is granular.

The thorax of *E. ornatus* is typical of the genus: it comprises eleven segments, the 7th and 10th of which carry strong, backward curving axial spines, each at least as long as the width (trans.) of the ring from which it originates.

The pygidium is triangular, ending in a stout, upturned spine the sides of which form an angle of 50 to 60 degrees; length and width are about equal (the largest measures about 17 mm.); the doublure width is about a tenth of the pygidial length.

The axis is about a third of the total width anteriorly, evenly tapering, comprising up to 35 rings on some of the largest pygidia. The first one or two rings, very rarely up to 6, are continuous; generally a smooth median space of $\frac{1}{3}$ the axial width starts behind the first ring. (This ring is confluent with the first pleural rib.) The number of axial tubercles ranges from 5 to 10 but in 90% of complete pygidia there are 7. A ring may carry 3 or 4 insignificant tubercles outside the smooth space but on the first ring a pair is invariably present. Only tubercles of the smooth central space were used in preparing text-fig. 1.

Pleural ribs of the pygidium, commonly 8 in number, are anteriorly about twice as wide (ex sag.) as the furrows and carry one row of large tubercles near the axis, and, anteriorly at least, a second, less conspicuous row further out; all ribs but the 8th are complete (pl. 124, fig. 12) and, on abraded specimens, are perforated at their outer ends like those of *E. punctatus* (Rosenstein, 1941, pl. 2, fig. 5) by a row of five or six minute tubuli. A line of similar perforations extends back on either side of the terminal spine.

Although 8 ribs is the rule, about 5% of individuals possess, on either side of the axial tip, a 9th pair of tubercles which are evidently situated on incomplete or rudimentary ribs (pl. 124, fig. 12). Only one pygidium (pl. 124, fig. 16) out of 900 definitely possesses 9 ribs of which 8 are complete (to the margin); two others are asymmetrical, with 9 complete ribs on the right side and 8 on the left.

The whole outer surface of the pygidium is finely granular, though generally this detail is best seen on the margins and doublure.

Rib tubercles are present in two irregularly zig-zag series. The outer one is so

irregular and consists of such minor tubercles that its details can be ignored; those of the inner series may be practically linear (pl. 124, fig. 19) but commonly one of the first four (the third as a rule) is displaced distally far out of line. No more than ten percent of pygidia in which the first axial tubercle is on the second ring have the second rib tubercle displaced distally, whereas if the first axial tubercle is on the first ring (pl. 124, fig. 13) at least sixty percent of pygidia have the second rib tubercle lying distally. There is, therefore, strong evidence that the location of axial and rib tubercles is interrelated and not as haphazard as it appears to be at first sight.

Axial tubercles obviously tend to be developed on every fourth ring starting with the second (text-fig. 1) although, as mentioned above, the regularity decreases posteriorly. Of the first 250 specimens only 37 have all six "modal rings" (2, 6, 10, 14, 18, 22) occupied: another 8 exhibit similar tetrad regularity on rings 3, 7, 11, 15, 19, 23 or 1, 5, 9, 13, 17, 21. The majority, although they tend either to follow the tetrad rule or, having started off "on the wrong ring," so to speak, tend to utilize the modal rings anyhow, may reduce or increase the spacing once or twice, may interpolate an extra tubercle here and there, or have groups of two or three on a ring instead of singly. One pygidium has the first six tubercles on every third (2, 5, 8, 11, 14, 17): none has constant spacing of a tubercle on every fifth ring, nor does any consistently alternate the spacing.

According to Rosenstein (1941, p. 61) the following rule is applicable to more than 98% of *Encrinurus punctatus:*

I. Pygidia with the distal tubercle on the third rib have the first four axial tubercles on rings 2, 5, 9 (rarely 8 or 10), 13 (or 14), or on 2, 6, 10, 14, etc.

II. Pygidia with a distal tubercle on the second rib have the first four axial tubercles on either 1, 4, 8 (or 7), 12 (or 11) or on 1, 5, 9 (or 8), 13 (or 12). These were the only pygidia on which she observed 9 pleura and 8 axial tubercles.

In general, these rules apply very well to *E. ornatus* but we have a group here in which the first tubercle is situated on the third ring: this has no parallel in *E. punctatus* but does appear to be similar to *E. shelvensis* Whittard (1938). Nevertheless, the "internal consistency" of the numbers of specimens in table I (e.g., the numbers of pygidia in column 1 and in row 3 in both carbonates and shales) suggests strongly that there are no grounds for separating off such groups as species.

For some time the writer was inclined to place the species represented by this collection in synonymy with *E. reflexus* Raymond but that species is too large and is represented only by three rather poorly preserved pygidia. *E. anticostiensis* Twenhofel is closely related, but has too long a terminal spine.

The forty pygidia from Mt. Vernon, Iowa, which Norton (1895) assigned to *E. ornatus* include larger specimens (up to 23 mm. long) than any found here or in the type area in Ohio: the distribution of axial tubercles, too, is more variable; he says (ibid., p. 81) that "no law obtains as to the successive number of the intervening segments." Some difference is to be expected between local populations of the same species, but whether each should be assigned formal status depends on the degree of stratigraphic or systematic precision with which they must be used. For the present no useful purpose would be served by splitting.

The large collection (175 pygidia) of *E. punctatus* which was described by Rosenstein (1941) affords some striking parallels with this one, but the two species are easily distinguished: the cephalon of *E. ornatus* has more tubercles and they are less regularly arranged; also, at least 17 percent of the Lockport pygidia have the first axial tubercle on the third ring and the relative frequencies of intervals of 4 rings to 3 rings from first to second tubercle, (.668 to .332, respectively, in *E. ornatus*), is apparently reversed in *E. punctatus* (.314 to .686 respectively: ibid. p. 60): that is, the spacing of anterior axial tubercles is closer in *E. punctatus*.

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# THE ANATOMY AND MORPHOLOGY OF CERTAIN CORDAITES LEAVES[1]

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ABSTRACT—Considerable taxonomic confusion exists in the nomenclature of *Cordaites* leaves. Among impression and compression forms such questionable features as size, shape, and ribbing patterns have been used. Among petrifactions, the amount and distribution of hypodermal sclerotic masses, the sequence and distribution of xylem development, the degree of differentiation of the mesophyll, and, in some cases, epidermal patterns have been used. This study is an attempt to correlate as many of these characteristics as possible using *Cordaites* leaves contained in Iowa and Kansas coal balls. Two species are recognized, *Cordaites principalis* (Germ.) Gein. (*C. affinis* of Reed and Sandoe) and *C. crassus* Ren. The internal structure of these is described in detail and correlated with the epidermal and ribbing patterns of each. An anatomical key to the leaf species of *Cordaites* which have been so described to present is provided.

## INTRODUCTION

PLANTS of the extinct gymnosperm genus *Cordaites* were very prominent constituents of most Carboniferous age floras. They were tall forest trees frequently reaching a height of 30 meters, with slender trunks rising upward for a considerable distance before giving rise to a crown of branches bearing spirally arranged, sessile leaves. These leaves are found abundantly as fossilized impressions, compressions, and petrifactions especially in Pennsylvanian age strata. Most of the early taxonomic work attempted the classification of the impression and compression leaf material on the basis of external form and ribbing patterns, and a vast number of specific names was instituted. Relatively few cordaitean leaf species have been described in terms of their internal structure, a situation which Reed and Sandoe (1951) ascribed to an apparent anatomical uniformity of the leaves in petrifactions. Only a very small number of cordaitean leaf species have had their epidermal structure determined. Both the external morphology and internal anatomy of some species, such as *C. principalis*, *C. lingulatus*, and *C. angulosostriatus*, have been determined, but to our knowledge only the study by Reed and Sandoe (1951) on a supposed new species, *C. affinis*, has previously attempted to actually correlate the external ribbing and epidermal pattern of a species with the internal anatomy.

There is considerable uncertainty at present regarding the validity of many of the described cordaitean leaf species recorded in the literature. Many compression species, especially those from American localities described by Lesquereux and Dawson, were established upon very fragmentary or poorly preserved material. The slight variations in leaf shape and ribbing which sometimes have been used as distinguishing taxonomic features may frequently be merely a reflection of foliar polymorphism or of varying states of preservation. There is a need to relate the anatomically described species from petrifactions with the form species described from impression and compression material. A broader combination of taxonomic criteria appears to be necessary to eliminate the present confusion and delimit the truly valid species.

The present study was an attempt to gain further insight into the taxonomic problems of cordaitean leaf classification, by ascertaining and correlating the internal anatomy, the external morphology, and the epidermal structure of certain cordaitean leaf species found in Iowa and Kansas coal balls.

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## REVIEW OF LITERATURE

*Generic Nomenclature and Classification.*—Leaves now referred to *Cordiates* were originally placed in the genus *Flabellaria* by Sternberg in 1823, who considered them related to the palms. Corda disproved this supposed relationship to the monocotyledons, and in 1850 Unger instituted the new generic name of *Cordaites*, honoring Corda's work. Subsequent investigators, notably Grand'Eury (1877) and Renault (1879), confirmed the gymnosperm nature of *Cordaites*.

The generic name of *Cordaites* is primarily applied as the organ genus of the leaves, with the other plant parts designated under a variety of organ genera. However, in its broad sense as the original generic name, *Cordaites* should include the whole plant once the various parts have been correctly associated.

Present day classification schemes place the genus in the family Cordaitaceae, of the fossil order Cordaitales, whose exact relationship to other gymnosperms is still rather obscure, but contemporary and perhaps of common origin with the pteridosperms and rather closely related to the Ginkgoales and Coniferales.

*General External Morphology.*—Cordaitean leaves were simple, entire, and quite coriaceous. They were characterized by close parallel venation from base to apex, with the veins dichotomizing inconspicuously at intervals to adjust to different lamina widths. The distance between adjacent veins varied from species to species.

There was a great variation in the size and shape of the leaves, although most commonly they were long and broadly linear, often reaching a meter in length. Others were lanceolate, oblanceolate, spatulate, or obovate in form, with acute, acuminate, or obtuse apexes (Arnold, 1947). Often they were inrolled, possibly accounting for the common inbricated condition found in fossils. Occasionally the apex was shredded. According to Dawson (1871) and Lesquereux (1878) the leaves were generally attached to the stem by a broad, inflated, semi-clasping base.

The subgeneric names of *Eu-Cordaites*, *Dory-Cordaites*, and *Poa-Cordaites*, instituted by Grand'Eury (1877) and based upon external leaf forms and ribbing patterns, are often used in classifying cordaitean leaf species of impression and compression material. These subgenera serve a useful descriptive purpose, even though it is recognized that they may have only limited taxonomic meaning (Seward, 1917). *Eu-Cordaites*, or the typical *Cordaites* in its more limited usage, referred to generally large and relatively broad leaves of varied shapes, with obtuse or rounded apexes, and fairly widely spaced equal or unequal ribs. *Dory-Cordaites* referred to variously sized, narrowly lanceolate, non-fleshy leaves, with pointed apexes and fine equal ribs. *Poa-Cordaites* referred to very narrow, fleshy leaves, never exceeding 1 cm. in width, with obtuse apexes and equal unbranched ribs.

Renault and Zeiller (1885) instituted another subgeneric name, *Scuto-Cordaites*, to refer to some leaves with unequal ribs, round contracted bases, and narrowly shredded distal portions. The additional subgeneric name of *Dictyo-Cordaites* was originated by Dawson (1890) to refer to some ribbon-like leaves with broad bases, unevenly truncate

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### EXPLANATION OF PLATE 125

FIGS. *1*—Cross section of *Cordaites principalis* proximal form showing both crushed and uncrushed areas, ×30.

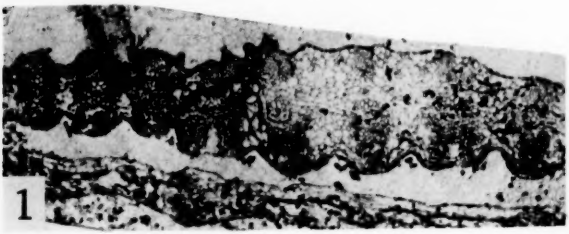
*2*—*C. principalis* attached to small stem of *Mesoxylon birame*, ×7.

*3*—Cross section of *C. principalis* non-proximal form, ×90.

*4*—Oblique sagittal section of *C. principalis* showing upper epidermis at top, compact mesophyll, and separated mesophyll plates at bottom, ×45.

*5*—Abaxial surface of *C. principalis*. Note alternation of intermediate and primary ribs, ×7.

*6*—Cross section of *C. principalis* leaf base, ×9.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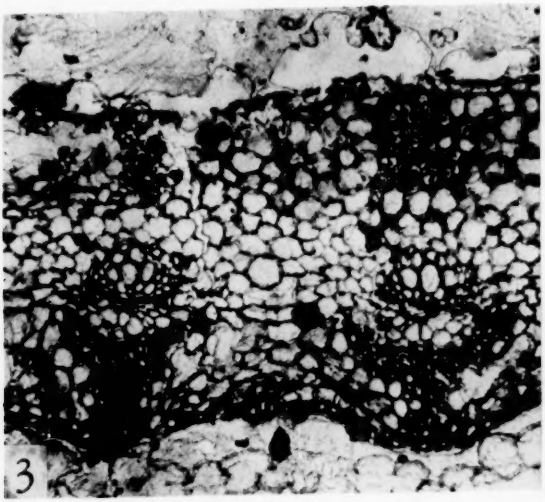
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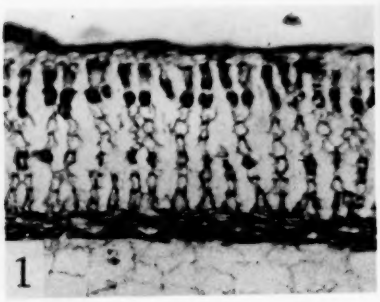
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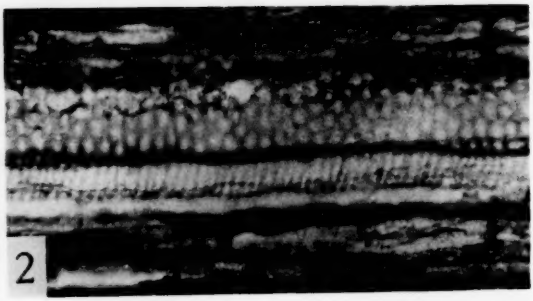
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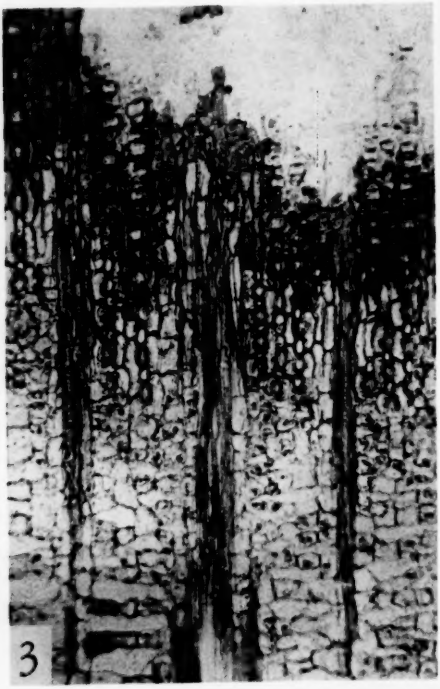
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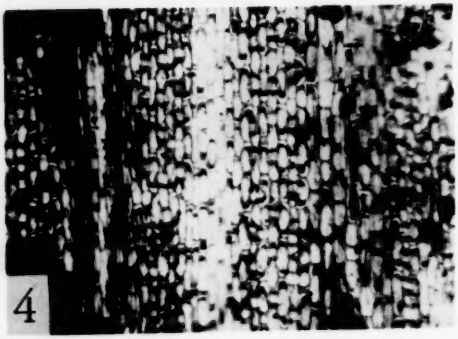
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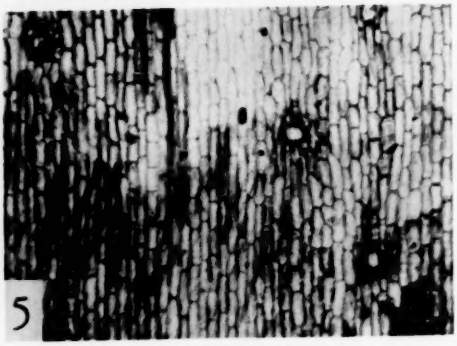
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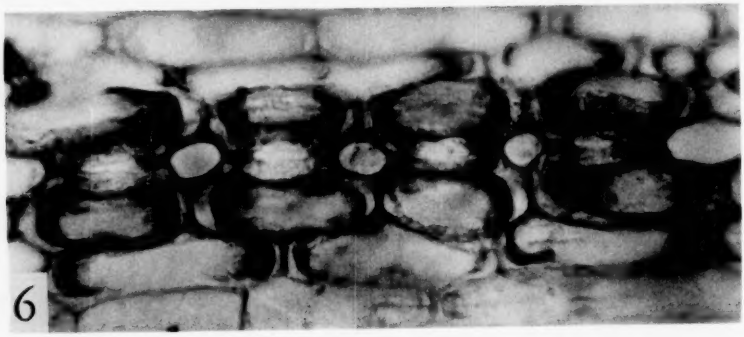
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apexes, and distinct acutely forked veins.

*General Epidermal Structure.*—Although the form and ribbing patterns of cordaitean leaf species have received much attention in impressions and compressions, a knowledge of their epidermal characteristics is rather meager. The leaf epidermis was covered with a moderately thick cuticle. The epidermal cells were rectangularly shaped, usually being several times longer than broad, with rather thick straight walls, as seen in superficial view. The cells were arranged lengthwise in regular rows parallel to the veins, and sometimes bore hairs or papillae.

On the lower epidermis the stomata usually appeared in definite stomatiferous bands, whose relative width varied in different species. The stomatal distribution within a stomatiferous band varied, but frequently they were borne in regular stomatal rows.

The stomata were oval-shaped and elongated in a direction parallel to the veins. The somewhat submerged guard cells were surrounded by 4–6 subsidiary cells, 2 of them polar and attached to the ends of the guard cells. Florin (1931) stated that the stomatal apparatus of *Cordaites* was haplocheilic of the monocyclic type, with the stomal mother cells having divided once to form the 2 guard cells, and the perigene epidermal cells functioning directly as subsidiary cells without dividing to form radial rows of encircling cells. The subsidiary cells sometimes bore papillae or cuticular ridges which were useful in specific diagnosis.

Only Wills (1914) has reported stomata as being present on the upper epidermis, indicating that they were few in number, smaller than on the lower epidermis, arranged in rows parallel to the venation, and frequently surrounded by 4 subsidiary cells forming a thickened ring around the sunken guard cells. Wills stated that the upper epidermal cells were thicker walled than the lower, and that circular structures of unknown significance were sometimes present. Whitefored (1916) also reported these circular openings to be present in a supposed *Cordaites* leaf from Nebraska and suggested the possibility of their having been hydathodes.

*General Internal Anatomy.*—Although most species were basically rather similar in their internal structure they differed somewhat in various anatomical features. Some species had well-differentiated palisade and spongy mesophyll regions, while in others the mesophyll was more uniform. In most species there was considerable lacunar tissue.

Well developed hypodermal masses of sclerotic tissue were almost invariably present, but their position and extent varied considerably in different species. Sometimes the hypodermal fiber strands were present only above and below the veins, at other times between the veins in various arrangements and amounts, and occasionally in bands reaching from one epidermis to the other between the veins.

The veins were usually enclosed by a well defined outer sheath of thin walled cells. Early workers often interpreted a layer of tracheid-like cells just within the outer sheath in many species as an "inner sheath of primitive transfusion tissue." Stopes (1903) considered this "inner sheath" as developed from the centripetal xylem, while Benson (1912) regarded it as probably a part of, or derived from, the centrifugal xylem. Seward (1917) questioned that this

EXPLANATION OF PLATE 126

FIGS. *1*—Radial section of *C. principalis* mesophyll, ×85.
*2*—Sagittal section of *C. principalis* showing reticulate and scalariform centripetal tracheids, ×350.
*3*—Oblique sagittal section of *C. principalis* correlating epidermal pattern with internal anatomy, ×98.
*4*—Abaxial epidermis of *C. principalis* ×45.
*5*—Adaxial epidermis of *C. principalis* ×90.
*6*—Row of stomata on abaxial epidermis of *C. principalis*, ×500.

inner sheath could really be distinguished from the true xylem elements.

The xylem has generally been considered to be mesarch, with the central protoxylem elements giving rise to a prominent strand of large centripetal tracheids above, and an irregular crescent of narrower centrifugal tracheids below. In some leaves, or parts of leaves, the centrifugal xylem remained undeveloped, hindering the detection of the mesarch protoxylem condition. The phloem, not often well preserved, was located below the centrifugal xylem. Despite a very common misconception that the xylem of all *Cordaites* leaves was mesarch, a careful perusal of original species descriptions reveals an exarch xylem condition, with centrifugal tracheids absent, as no less frequent.

The vascular arrangement varied somewhat in the different species that have been anatomically described, although in many of the specimens studied, the preservation was too poor to allow for a very accurate determination of the xylem and phloem condition.

*Criteria for Species Determination.*—Paleobotanical classification of non-petrified fossils is, at best, rather arbitrary, being of necessity based entirely upon morphological criteria, and complicated by such special problems as fragmentary plant parts and fossilization changes. These difficulties have led to the paleobotanical practice of maintaining as distinct form species each morphological variant encountered, until organic connections have verified their identity as the same species.

Specific determination of cordaitean foliage in impression and compression material has been based traditionally upon leaf shape and the arrangement of the course and fine ribs on the leaf exterior. Species have been distinguished upon differences in rib frequency, the number and distinctness of intermediate striae between the main ribs, and differences between the upper and lower surfaces. However, it is realized that leaf shape and ribbing are rather variable characters upon which to base classification, since foliar polymorphism was probably not uncommon, and the rib frequency was known to vary in different leaf parts, and in leaves of different sizes and ages. The presence of intermediate striae marking the location of internal sclerotic bands was probably too dependent upon fossilization conditions to be a very reliable taxonomic feature. Alhough leaf width had been considered rather important, Reed and Sandoe (1951) showed that the width of a leaf as it appeared on a rock surface may be only a fraction of the width of an originally inrolled or imbricated leaf.

The use of internal anatomy as revealed in petrifactions is an important additional taxonomic aid. Anatomical features used in classification include leaf thickness, vein frequency, the position and extent of the hypodermal sclerotic bands, the degree of palisade and spongy mesophyll differentiation, and the vascular bundle arrangement. Darrah (1940) has pointed out that anatomical studies do have taxonomic limitations, since different leaf portions may have varied considerably in their degree of tissue development, making it necessary to know from which leaf part a section was made. Such a case was illustrated when Benson (1912) concluded that 3 separate cordaitean leaf species established by Felix (1886) upon anatomical characteristics, were in reality different parts of the same leaf form. Another taxonomic limitation results from anatomical differences between leaves of different ages. This latter problem was approached by Lignier (1913) who made histological studies upon a *C. lingulatus* bud showing the tissue ontogeny from very young to adult leaves of the same species. In using anatomical criteria, it must be realized that vertical compression during the fossilization process may have considerably distorted the leaf thickness, the distance between the bundles if the leaf were not in a horizontal plane in the matrix (Reed and Sandoe, 1951) and perhaps even the original cell shapes (Walton, 1936).

The use of epidermal characters, especially of the stomatal structure and arrangement, has opened another valuable taxonomic approach. Florin (1931), after a study of the cuticles of both fossil and living gymnosperms, including certain cordaitean leaves, concluded that epidermal and stomatal features in combination with the usual morphological approach constitute a complex of features valuable in generic and

specific determination. Epidermal features which have been considered of taxonomic value with reference to cordaitean leaves were the relative width of the stomatiferous and nonstomatiferous bands, the shape of the epidermal cells in both bands, the stomatal arrangement within a band, the arrangement and size of the subsidiary cells surrounding the guard cells, the stomatal frequency, and the presence of special epidermal structures such as hairs, papillae, or cuticular ridges.

It is recognized that each of the criteria which have been previously used to delimit species possess individual limitations, causing considerable taxonomic confusion. This problem was reflected by Arnold (1941) when he stated that "the difficulties attending the identification of cordaitean foliage are mainly responsible for the widespread neglect of them on the part of paleobotanists."

The most reliable approach in the systematics of cordaitean leaves would appear to be the simultaneous use of as many different criteria as possible. This has been attempted in the present study through the use of coal ball petrifactions which can reveal the external ribbing pattern, the internal anatomy, and the epidermal structure of the same leaf. Coal balls are limited, however, in seldom revealing the over-all length of the long cordaitean leaves.

*Impression and Compression Species.*—Space does not permit a discussion of the many impression and compression species that have been described. According to the U. S. Geological Survey Index to Paleobotanical Species approximately 60 species have been recorded. Suffice it to say that many of these were established upon very fragmentary or poorly preserved material, or were imperfectly described and figured in the literature, with even the location of the early type specimens frequently unknown. Three common compression species, *Cordaites principalis* (Germ.) Gein., *C. lingulatus* Gr.'Eury and *C. angulosostriatus* Gr.-'Eury, will be discussed in some detail later since their internal anatomy is also known.

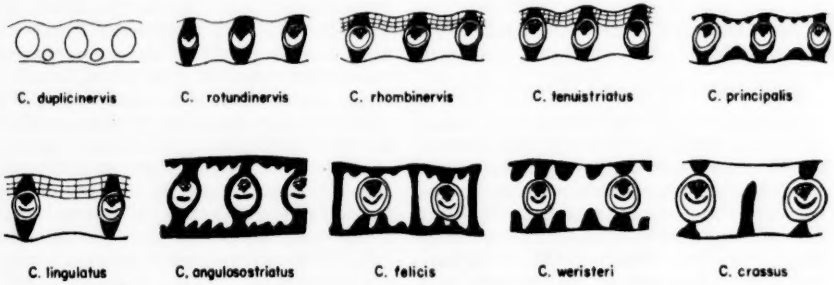
*Anatomical Species.*—The number of species described on the basis of internal structure is, of course, much less than in the previous category. A brief description of each follows, and text-fig. 1 illustrates the dominant features of each.

CORDAITES DUPLICINERVIS Gr.'Eury

Very small, thin, narrow, delicate leaves with markedly inrolled borders often forming pronounced spirals; veins unequal in size, with large central bundles alternating with smaller bundles appearing only on one side. (A questionable and poorly described species.) Carboniferous of France.—Grand-'Eury (1877).

CORDAITES ROTUNDINERVIS Gr.'Eury

Hypodermal sclerotic tissue limited to triangular masses above and below the veins abutting to the bundle sheath; mesophyll not differentiated into definite palisade and spongy regions but somewhat more compact adaxially; lacunae oriented perpendicularly to veins; exarch xylem arrangement; triangular wedge of tracheids radiating up-




TEXT-FIG. *1*—Generalized cross-sectional views of the various anatomical species of *Cordaites*. Dark areas represent hypodermal sclerotic masses.

ward from inferior protoxylem point; lower epidermal pattern with stomata not aligned in definite rows but about 6 encountered across the width of a stomatiferous band. Carboniferous of France.—Grand'Eury (1877), Seward and Sahni (1920).

CORDAITES RHOMBINERVIS Gr.'Eury

Hypodermal sclerotic tissue limited to triangular masses above and below the veins abutting to the bundle sheath; mesophyll apparently differentiated into definite palisade and spongy regions, the palisade cells evenly arranged and nearly isodiametrical; exarch xylem arrangement, triangular wedge of scalariform and pitted tracheids radiating upward becoming progressively larger from inferior protoxylem point; bundle sheath of longitudinally elongated, somewhat pitted elements; about 25 veins/cm.; superficial ribbing distinct. Carboniferous of France.—Grand'Eury (1877), Renault (1879).

CORDAITES TENUISTRIATUS Gr.'Eury

Hypodermal sclerotic tissue limited to triangular masses above and below the veins abutting to the bundle sheath; mesophyll apparently differentiated into palisade and spongy regions, the palisade cells nearly isodiametrical, evenly arranged, and darkly colored, the spongy mesophyll composed of transversely elongated cells and lacunae; exarch xylem arrangement, triangular wedge of scalariform and pitted tracheids radiating upward becoming progressively larger from inferior protoxylem point; bundle sheath of large, darkly-colored, somewhat pitted elements; about 17 equally spaced veins/cm.; superficial ribbing distinct; upper epidermal cells bearing papillae. Carboniferous of France.—Grand'Eury (1877), Renault (1879, 1881).

CORDAITES PRINCIPALIS (Germ.) Gein.

A common widely distributed compression as well as anatomical form; narrowly lanceolate in shape exceeding 50 cm. in length but not exceeding 4 cm. in width with the broadest portion at $\frac{2}{3}$ the distance from the base; apex blunt, sometimes split into segments; about 0.4 mm. thick; 14–22 veins/cm., anatomical descriptions by Renault and Stopes list 22/cm.; superficial ribbing distinct with a regular alternation of primary ribs with intermediate secondary ribs on the abaxial surface, and 1–5 finer intermediate striae on the adaxial surface; external ribbing resulting from triangular masses of hypodermal sclerotic tissue above and below the veins abutting to the bundle sheath, a fairly prominent intermediate abaxial sclerotic strand between the veins, and 1–5 smaller irregular adaxial sclerotic groups; mesophyll reported by Renault as differentiated into palisade and spongy regions, but Stopes indicates this distinction to be rather obscure except in radial sections; exarch xylem arrangement, triangular wedge of tracheids radiating upward becoming progressively larger from the inferior spiral protoxylem tracheids to the large pitted tracheids above; bundle sheath of 2–3 layers of longitudinally elongated thin-walled elements, sheath widest above the bundle; a rather complete "inner sheath" of tracheids reported as present along sides and under the phloem. Carboniferous and Permian of Europe, compression form in North America.—Germar (1848), Geinitz (1855), Renault (1879), Stopes (1903); also in Kidston (1893), Arnold (1949).

CORDAITES LINGULATUS Gr.'Eury

A well known compression as well as anatomical form; obovate shape, bluntly rounded almost truncate apex, up to $11 \times 35$ cm. with basal width of 4 cm.; superficial ribs in basal portion unequally prominent with 1–3 secondary intermediate ribs, but becoming equally prominent distally; internal hypodermal sclerotic tissue limited to triangular masses above and below the veins abutting to bundle sheath; mesophyll clearly differentiated into distinct palisade and spongy regions with considerable lacunar tissue; about 17 veins/cm; mesarch xylem arrangement, central centripetal strand of large scalariform, reticulate and pitted tracheids with spiral protoxylem tracheids at its lowest point, centrifugal xylem a crescent of small reticulate or pitted tracheids below; scattered "inner sheath" tracheids found laterally just within bundle sheath; papillae present on lower epidermal cells. Carboniferous and Permian of Europe. —Grand'Eury (1877). Renault (1879, 1881), Stopes (1903), Lignier (1913), Florin (1931).

CORDAITES ANGULOSOSTRIATUS Gr.'Eury

A well known compression as well as anatomical form; spatulate in shape with broadly rounded apex, 10–15×60–100 cm.; superficial surface coarse and uneven; very thick (about 1 mm.) and fleshy; well developed hypodermal sclerotic masses above and below the veins abutting to the bundle sheath; 3 almost equally developed intermediate sclerotic ribs opposite in position on abaxial and adaxial sides; mesophyll not differentiated into palisade and spongy layers, although adaxially the mesophyll more compact and darkly colored, lacunar tissue present; veins large, about 17/cm.; mesarch xylem arrangement; small spiral protoxylem elements in center, a mass of large scalariform and pitted centripetal tracheids above, an arching group of small pitted centrifugal tracheids below; a well-defined bundle sheath several layers thick of sclerotic elements, a unique feature among *Cordaites* leaf species; lower epidermal pattern with stomata arranged in regular single rows separated by alternately wide and narrow nonstomatiferous bands. Carboniferous and Permian of Europe; compression form occasionally reported from North America.—Grand'Eury (1877), Renault (1879), Scott (1909), Seward and Sahni (1920).

CORDAITES CRASSUS Renault

(Darrah mistakenly attributed authorship to Grand'Eury.) Thick fleshy leaves; superficial surfaces relatively smooth; 14 veins /cm. according to Renault, although Darrah indicates greater vein frequency and less regularity with veins frequently paired; hypodermal sclerotic strands associated with veins usually not attaching to bundle sheath, a large intermediate abaxial sclerotic strand usually extending more than half way across the leaf thickness, and smaller intermediate adaxial masses opposite the larger abaxial ones depicted by Darrah but absent according to Renault; mesophyll not differentiated into palisade and spongy regions although more compact toward the adaxial side; xylem mesarch, composed of an upper centripetal mass and lower centrifugal arc, but no "inner sheath" elements present; lower epidermal pattern of narrow nonstomatiferous bands alternating with wide stomatiferous bands containing 4–6 longitudinal stomatal rows, stomatal frequency of 150 /mm.$^2$, no papillae. Carboniferous of France and Iowa.—Renault (1879), Seward and Sahni (1920), Darrah (1940).

CORDAITES FELICIS Benson

Basal thickness of 1 mm. decreasing upward; about 15–21 veins/cm.; an intermediate sclerotic strand extending completely across the leaf thickness about midway between the veins; thick proximal regions with almost continuous abaxial and adaxial hypodermal sclerotic layers, these layers interrupted in thinner portions to form small masses varying in size and number, sclerotic masses often but not always abutting to the bundle sheath; mesophyll not differentiated into palisade and spongy regions although more compact adaxially; mesarch xylem arrangement, well-developed upper centripetal xylem mass of large pitted tracheids radiating upward from lower protoxylem group, inferior crescent of centrifugal xylem; thick bundle sheath of longitudinally disposed elements; "inner sheath" tracheids lining lower part of bundle sheath. Carboniferous of British Isles and northern Europe; reported by Darrah (1941), probably erroneously, from Iowa.—Benson (1912), Felix (1886), Seward (1917), Scott (1923), Koopmans (1928).

CORDAITES WERISTERI Leclercq

(Found closely associated with and may be a variant form of *C. felicis*.) Leaf fleshy, 0.5–1.4 mm. thick; almost equal hypodermal sclerotic masses lining both surfaces, none jutting very far inward; the masses varying in number, but always opposite on abaxial and adaxial sides, the abaxial masses somewhat more developed, often but not always contacting the bundle sheath; mesophyll not differentiated into palisade and spongy regions, the lacunar tissue highly developed and complex except in proximal regions; a distinct bundle sheath 2–3 cell rows thick; mesarch xylem arrangement, with triangular wedge of centripetal tracheids in upper vein region radiating from spiral protoxylem elements at its lower tip, centrifugal xylem tracheids forming a crescent below. Carboniferous of Europe.—Leclercq (1927), Koopmans (1928).

CORDAITES AFFINIS Reed and Sandoe *non* Gr.'Eury

(A homonym; specific epithet used by Grand'Eury (1877) for unrelated compressions species. Probably conspecific, as will be shown, with *C. principalis*.) Leaf shape and length unknown; width up to 4.5 cm.; superficial ribbing distinct with regular alternation of primary with intermediate secondary ribs on abaxial surface, and 2–3 or more intermediate secondary striae between primary ribs on adaxial surface; external ribs resulting from internal triangular masses of hypodermal sclerotic tissue above and below the veins abutting to the bundle sheath, a fairly prominent intermediate abaxial mass, and 2–3 small intermediate adaxial masses; mesophyll reportedly separated into palisade and spongy layers but distinction obscure except in some radial sections; spongy mesophyll near abaxial side often lacunar; xylem elements in upper part of vein, and authors assumed without evidence a mesarch xylem arrangement; phloem below; well-defined 1–3 layered bundle sheath of thin-walled elements; lower epidermal pattern of alternating nearly equal stomatiferous and nonstomatiferous bands, the former composed of about 3 (2–5) longitudinal stomatal rows in each furrow between successive hypodermal sclerotic bands. Carboniferous of Iowa.—Reed and Sandoe (1951).

## METHODS AND MATERIALS

The cordaitean leaves examined in this study were obtained from Kansas and Iowa coal balls. Coal balls with K.S.T.C. collection numbers of 28, 504, 508, 510, 511, 530, 535, 648, 714, and 1373 were obtained from the Pittsburg and Midway Coal Co. mines near West Mineral, Kansas, a locality assigned to the Fleming Coal of the Cherokee Group, which occurs slightly below the middle of the Des Moines Series of the Pennsylvanian. Coal balls with K.S.T.C. numbers 245 and 260, and University of Minnesota numbers 1054 and 1288 were obtained from the What Cheer Clay Products Co. mine area near What Cheer, Iowa, a locality geologically ascribed to the lower portion of the Des Moines Series. Coal balls with U. of Minn. numbers 607, 609, 858, 870, 997, 1004, 1035, 1042, 1044, 1092, 1099, 1103, 1117, and 1121 were obtained from the Carbon Hill mine; 622, 767, and 1126 were obtained from the Old Atlas mine; and 784 and 785 were obtained from the Ellis mine. All of these are located in the Oskaloosa and Ottumwa, Iowa, area and also ascribed to the lower portion of the Des Moines Series.

During the course of this study it was necessary to determine the superficial ribbing pattern, the internal anatomy, and the epidermal structure of the various leaves. The superficial ribbing pattern of a leaf was revealed by fragmenting the coal ball with hammer and chisel in such a way that the cleavage plane revealed the leaf surface.

Internal sections were obtained by using the cellulose acetate film peel technique and thin sections. At least 3 kinds of internal sections were made of each individual leaf examined, in as many different leaf portions as possible. These included transverse sections perpendicular to both the blade surface and the vein courses, radial sections perpendicular to the blade surface and parallel to the vein courses, and sagittal sections parallel to the blade surface. Various oblique sections were also attempted in the hope that they might shed further light on the leaf anatomy.

Whenever satisfactory internal sections of well-preserved leaves had been obtained, the maceration technique, employed extensively by Florin (1931) on other gymnosperms, was used to determine their epidermal structure. A small part of the coal ball containing a portion of the single leaf was chipped off and placed in dilute HCl. As the limestone matrix dissolved, the acid resistant cuticles were allowed to separate freely. By careful use of dissecting needles both the upper and lower cuticles could often be separated simultaneously.

## RESULTS AND DISCUSSION

### CORDAITES PRINCIPALIS

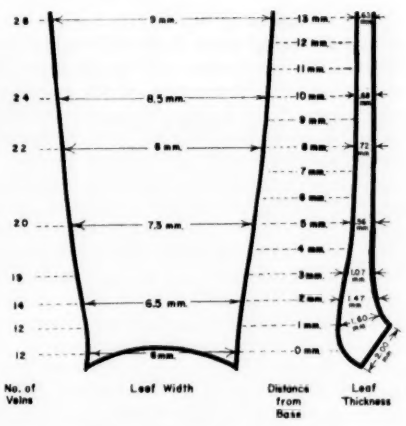
*Occurrence.*—Coal balls 28, 504, 508, 510, 530, 535, 648, 714, and 1373 from West Mineral and coal balls 245, 260, 1054, and 1288 from What Cheer contained large numbers of leaves that could be identified as belonging to the species described by Reed and Sandoe (1951) as *C. affinis*, but which, as we will show, is probably conspecific with *C. principalis*. This species appeared to

represent the most common, and in fact the only clearly recognizable form of cordaitean leaves in the West Mineral and What Cheer coal balls investigated.

*External Morphology.*—As is the case with many other anatomical species, rather little is known about the over-all size and shape of these coal ball specimens. The width from margin to margin of 63 recorded leaves, ranged from 0.55–4.10 cm., with the number of veins varying from as few as 12 to as many as 60 in fairly direct correlation with the leaf width. This compares favorably with Reed and Sandoe's (1951) report that the widest leaf found by them was 4.5 cm. with about 60 veins. The longest fragment found in the coal balls was about 10 cm., but this appeared to be only a small fraction of the original leaf length, since only slight changes in leaf width and vein number occurred in the extent revealed. Since the width and venation changed so slightly, it is thought rather likely that this species might have consisted of very long, broadly linear leaves, perhaps over 50 cm. in length which very gradually widened from a basal width of a cm. or less to a width of about 4.5 cm. and then probably tapered again toward a completely unknown apex. Such a conjecture, however, is unsubstantiated by direct evidence.

The leaves, though sometimes rather flat, were usually incurved at the margins or inrolled to various degrees, as was reported by Reed and Sandoe, who indicated that the surface width visible might be misleading if ever found in compression material.

While splitting techniques quite frequently disclosed the leaf bases, identifiable apexes were never thus revealed. The well-preserved leaf bases were 0.6–1.2 cm. wide, and 1.5–2 mm. thick in the central region, giving somewhat the appearance of a flattened ellipse in transverse sections (plate 125, fig. 6). The variations noted in the width and thickness of these leaf bases appeared to be due, at least in part, to differences between young and mature leaves. Presumably young leaves, which were found attached to a small, terminal stem attributed to *Mesoxylon birame* Baxter (plate 125, fig. 2), were at the lowest extreme, and older leaves in which some basal secondary tissue has been identified were at the highest extreme of this




TEXT-FIG. 2—Reconstruction of *Cordaites principalis* leaf base indicating changes in number of veins, width, and thickness with increasing distance from base.

variation. The thickened base was somewhat recurrent with a slightly concave or semi-clasping adaxial surface, quite similar to Seward's (1917) description of the base of Germar's type specimen of *C. principalis*. The leaf narrowed slightly 1–2 mm. above the base and then widened steadily to reach about 1⅓ times its original width at 1 cm. above the base. Thereafter, the width seemed to gradually increase upward at a much less perceptible rate. The leaf thickness upward from the base was rather sharply reduced to about 50% of the original thickness in a 3 mm. distance, and another reduction of about 25% occurred during the next 3 mm. Thereafter, the lamina thickness tapered only very gradually to eventually reach the 0.3–0.5 mm. average thickness through the central rib regions that was most characteristic of the wider, non-proximal portions of the leaves. Text-fig. 2 represents a reconstruction of the basal region of a somewhat narrower than average *C. principalis* leaf. Transverse views at the leaf base revealed the characteristic form shown in plate 125, fig. 6, while transverse sections of the proximal leaf regions somewhat above the base revealed the form shown in plate 125, fig. 125 and transverse sections in non-proximal regions revealed the form shown in plate 125, fig. 3.

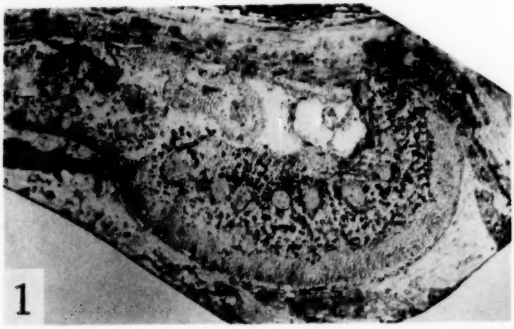
The thickness of the leaves varied, undoubtedly being quite dependent upon the degree of preservation. All leaves tapered somewhat in thickness toward the margins, which were 0.1–0.3 mm. thick with bluntly rounded instead of tapered ends. Although some well-preserved leaves were more-or-less uniform in thickness, most had the inter-rib regions crushed or pinched inward to varying degrees (plate 125, fig. 1). In many leaves the thickness of the inter-vein regions was only about ½ of that across the veins, while in a few the inter-vein regions were so crushed that in transverse sections the leaf resembled a series of beads on a string. These variations probably have little significance other than illustrating differences in compression during the preservation process. It can be readily seen that the degree of inter-vein crushing affects the degree of prominence of the external ribs.

The primary superficial ribs were caused by hypodermal sclerotic tissue associated with the veins which resisted the crushing that depressed the inter-vein regions. The intermediate ribs were produced by hypodermal strands of sclerotic tissue between the veins. The 92 leaves recorded showed a considerable variation in primary rib (or vein) frequency from 13–28/cm. There proved to be a definite correlation between total leaf width and the number of primary ribs (or veins)/cm. with narrow leaf sections having closer veins and wider leaf sections having more distant veins. Lamina widths of 0.55–1.2 cm. averaged 22.6 veins/cm., with a 0.44 mm. distance between the veins. These narrower sections were presumably near the base, as borne out by their increased thickness and, due to the more frequent dichotomizing of the veins, the not uncommon association of the primary ribs in pairs. Leaf sections of 1.3–1.9 cm. widths averaged 18.7 veins/cm., spaced at intervals of about 0.53 mm. Leaf sections of 2.0–2.9 cm. widths had an average of 16.5 veins/cm., or about 0.61 mm. apart. Leaf sections exceeding 3 cm. widths averaged 15.1 veins/cm. with a 0.66 mm. distance between the veins. It was further noted that the 2 broadest leaf specimens with widths of 3.8 and 4.1 cm. averaged only 13 and 14 veins/cm. respectively. Reed and Sandoe do not report the number of veins/cm. in their description, but it may be inferred from their report that a leaf 4.5 cm. wide had about 60 veins. This represents an average of 13.3 veins/cm. with the bundles about 0.75 mm. apart, placing it at the extreme end of the vein frequency range as observed above, but well within the range of expectation for a leaf of that width.

There seemed to be a tremendous variation in the degree to which intermediate ribs were evident on the superficial lamina surfaces, even on different parts of the same leaf specimen. The abaxial surface usually revealed a single, fairly distinct, but not overly prominent, intermediate rib about midway between the primary ribs (plate 125, fig. 5). However, this intermediate rib was not always evident, or, when present, occasionally fine striae were seen on either side of it. The greatest variation was noted on the adaxial superficial surface where either none, 1–3, or as many as 5 fine intermediate striae were evident between the primary ribs. The intermediate striae situated adjacent to the primary ribs seemed to be the most prominent, but none seemed continuous for any great distance. This compares exactly with the ribbing patterns determined by Reed and Sandoe for this species and, signifi-

EXPLANATION OF PLATE 127

FIGS. *1*—Cross section of *C. crassus* leaf base, ×10.
*2*—Cross section of leaf base vein of *C. crassus* with secondary xylem, ×85.
*3*—Cross section of proximal region of *C. crassus* with extensive intermediate sclerotic ribs, ×45.
*4*—Proximal region of *C. crassus* with sclerotic ribs extending completely across leaf, ×45.
*5*—Radial section of *C. crassus* showing vertical mesophyll plates and horizontal row of large parenchyma cells of non-proximal region, ×85.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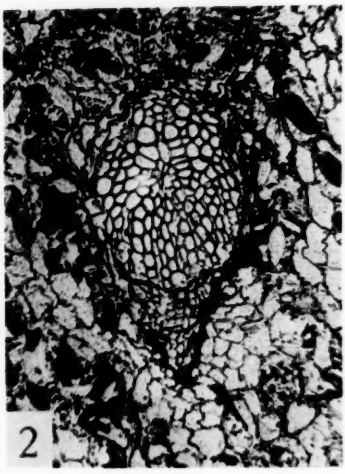
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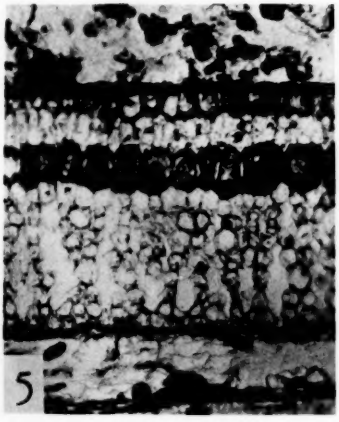
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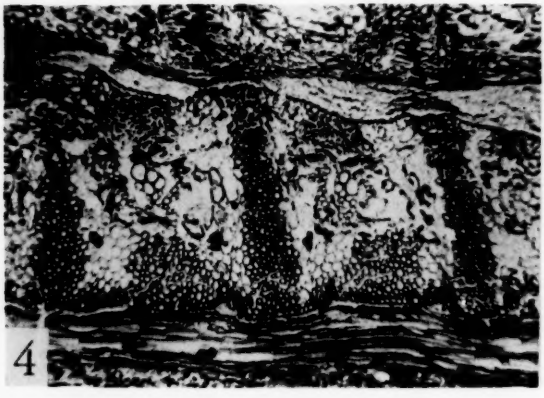
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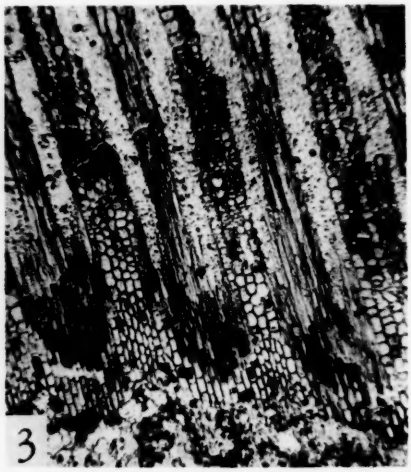
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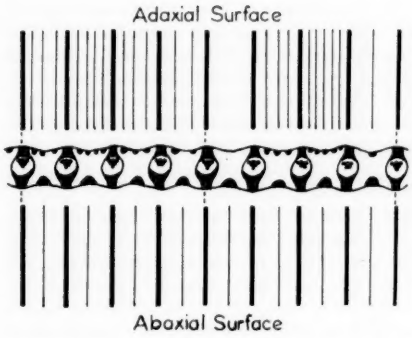
cantly, to those reported for compression specimens of *C. principalis* as well.

The extreme variability of the primary rib spacing and the visibility of intermediate superficial ribs as demonstrated in this study, tends to cast serious doubts upon the reliability of the extensive traditional reliance upon superficial ribbing patterns in cordaitean leaf classification of compression material.

*Internal Anatomy.*—It was possible to observe the etched transverse leaf sections and superficial ribbing patterns simultaneously under low magnification, and by such examination to clearly perceive the correlation of the superficial ribs with the hypodermal fibrous strands beneath each epidermal layer (text-fig. 3). This correlation was also revealed quite graphically by oblique sagittal sections (plate 126, fig. 3). Large sclerotic strands inferior and superior to the veins abutted against the bundle sheath and the epidermis except in basal regions, with the abaxial sclerotic masses somewhat more extensively developed (text-fig. 5). A rather prominent hypodermal sclerotic strand about 0.1–0.2 mm. wide and extending about 0.10–0.15 mm. into the mesophyll was located midway between the veins on the abaxial side usually causing the regular alternation of primary and secondary superficial ribs seen on the abaxial surface. Under the adaxial surface the arrangement of the hypodermal sclerotic tissue was more variable, but usually consisted of 2–5 small masses of fibers. These sometimes resulted in small superficial striae on the adaxial surface, but at other times seemed to have no observable effect, thus accounting for the variability found in the external ribbing pattern. Cuticles reveal that some fibrous




TEXT-FIG. 3—Correlation of adaxial and abaxial ribbing patterns with internal sclerotic masses in *Cordaites principalis*.

tissue underlaid much of the epidermis, but was extremely thin in stomatal regions. The sclerotic strands were composed of true fiber cells with walls 3–4 $\mu$ thick and lumens 3–25 $\mu$ in diameter. In slightly oblique transverse sections the lumens appeared almost obscured by the thick cell walls, but in true transverse sections the walls were revealed as much thinner and the lumens often relatively large. Longitudinal sections revealed the fiber cells to be tapered, often twisted, and elongated, averaging 0.65 mm. but occasionally reaching 2.5 mm. in length.

One of the more interesting aspects was the mesophyll arrangement. Transverse sections with well-preserved mesophyll revealed it as a rather uniform mass of fairly large, hexagonal parenchyma cells, without a palisade region being distinguishable, although the mesophyll near the adaxial side appeared slightly more compact (plate 125, fig. 3). Excessive crushing often resulted in

EXPLANATION OF PLATE 128

FIGS. *1*—Cross section of non-proximal region of *C. crassus* with large, dark-staining parenchyma cells on adaxial side, ×86.

*2*—Adaxial non-proximal epidermis of *C. crassus*. Note very occasional stomata and banded arrangement of cells, ×59.

*3*—Oblique sagittal section of *C. crassus* correlating adaxial epidermal bands with internal structure, ×45.

*4*—Abaxial epidermis of *C. crassus*, ×167.

the appearance of somewhat transversely elongated cells arranged in short strands or masses in the central mesophyll region. A frequently noted lack of mesophyll preservation in transverse sections was often rather surprising, since the vascular tissues of the same sections appeared well preserved.

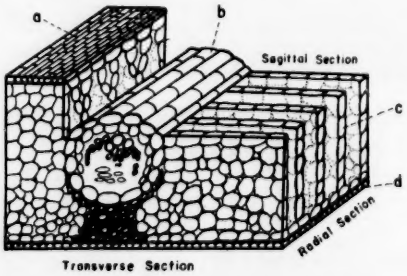
Radial sections revealed the mesophyll as anastomosing strands of variously shaped, but usually vertically elongated, parenchyma cells separated by large lacunae extending between the abaxial and adaxial side (plate 126, fig. 1). These strands seemed to be attached to compact parenchymatous layers against either epidermis. The strands often approached each other so closely near the adaxial side that about 3–4 fairly uniform cell layers appeared to form a palisade region, but with the lower layers beginning to be separated by slit-like lacunae. However, some radial sections revealed a complete separation of these strands even in this upper region. Reed and Sandoe's radial section drawing (1951, p. 452, fig. 16) does not represent the typical mesophyll condition as seen in the present study, but appears somewhat similar to radial sections of the more basal or marginal leaf regions.

Sagittal sections revealed the mesophyll as separate anastomosing strands of transversely elongated cells extending between the vascular bundles and attached to the bundle sheath or sclerotic masses. Plate 126, fig. 3 shows an oblique sagittal section revealing a single densely arranged layer of small parenchyma cells immediately adjacent to the lower epidermis with circular lacunar openings at each stomal position. Plate 125, fig. 4 represents a somewhat oblique sagittal section showing a compact layer of large hexagonal parenchyma cells located just below the upper epidermis. The intervening mesophyll region between these compact layers consisted of cell strands separated by progressively wider lacunae as one proceeded from the adaxial to the abaxial side. All oblique cuts between true radial and true sagittal sections also revealed the mesophyll as composed of apparent strands of cells, while oblique cuts between true sagittal and true transverse sections showed all variations between mesophyll strands, no mesophyll preservation, and rather compact parenchymatous tissue.

The conclusion is reached, therefore, that except at the leaf base and leaf margins, the mesophyll is normally composed of a series of anastomosing plates between the vascular bundles, oriented with their surfaces perpendicular to both the leaf surfaces and to the vein courses, as diagrammatically depicted in text-fig. 4. The similarity between the septate pith of mature cordaitean stems and the plate-like mesophyll of these leaves is noteworthy.

A clearly defined bundle sheath (text-fig. 5) composed of 1–3 layers of large, thin-walled cells enclosed the veins, and, except near the base, abutted directly against the inferior and superior sclerotic hypodermal strands. The sheath was broadest superior to the vein, consisting here of the largest elements with diameters of 25–80 $\mu$. The sheath narrowed to a single cell layer inferior to the vein, consisting here of smaller elements with diameters of only 18–35 $\mu$. The sheath cells were clearly distinguished from the surrounding mesophyll by being radially elongated in the direction of the veins, and arranged in even lengthwise rows. The cells appeared rectangular with very straight end walls, ranging from 40–160 $\mu$ in length as seen in longitudinal sections. The appearance of bordered pits on the walls of the sheath cells, as originally reported by Reed and Sandoe, was also verified in this study.

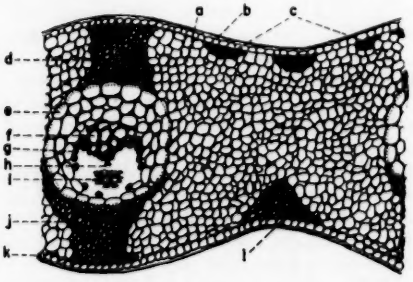
The protoxylem (text-fig. 5) was located in the central region of the vascular bundle and consisted of 1 or 2 very narrow spiral




TEXT-FIG. 4—Three-dimensional view of internal structure of *Cordaites principalis* to show arrangement of mesophyll plates. *a*, adaxial epidermis; *b*, bundle sheath; *c*, mesophyll plate; *d*, abaxial epidermis.

tracheids measuring 4–8 $\mu$ in cross-sectional diameter. It was usually separated from the metaxylem tracheids above by a layer of small rectangular xylem parenchyma cells measuring 3–5 $\mu$ in cross-section. The main mass of centripetal metaxylem consisted of a wedge-shaped core of progressively larger tracheids radiating upward from the protoxylem and ranged from the smaller scalariform to the larger reticulate or pitted elements (plate 126, fig. 2). The small metaxylem tracheids in the lower region of the centripetal xylem mass were 8–15 $\mu$ in diameter, while the largest tracheids located in the upper part of the bundles frequently reached diameters of 50 $\mu$. Longitudinal sections revealed that the largest scalariform tracheids often reached 1.5–2.0 mm. in length, while the even larger reticulate or pitted tracheids sometimes exceeded a length of 3 mm. Reed and Sandoe do not record the measurements of the xylem elements in their report, but the measurements of the present study compare closely with those reported by Stopes (1903) for *C. principalis*.

The wedge-shaped core of metaxylem described above was flanked on either side by a clustered group of 5–6 smaller tracheids, ranging from 4–12 $\mu$ in cross-sectional diameter. Each of these groups was subtended by a strand of small thick-walled tracheids extending downward along the sides of the phloem region. These strands usually were not continuous in the lower bundle regions but rather consisted of a few scattered tracheids around and below the phloem. Occasionally these formed a more-or-less continuous arc just within the bundle sheath enclosing the phloem region, but this was quite rare.




TEXT-FIG. 5—Transverse section of *Cordaites principalis*. *a*, mesophyll; *b*, adaxial epidermis; *c*, adaxial intermediate hypodermal sclerotic strands; *d*, superior hypodermal sclerotic cap above vein; *e*, bundle sheath; *f*, centripetal metaxylem; *g*, side tracheid strand or "inner sheath;" *h*, protoxylem; *i*, phloem; *j*, inferior hypodermal sclerotic cap below vein; *k*, abaxial epidermis; *l*, abaxial intermediate hypodermal sclerotic strand.

If the historical terminology proposed in early studies is strictly applied to this presently determined xylem condition of *C. principalis*, it may be assumed that the superior wedge-shaped mass of tracheids represents the centripetal xylem, and the side tracheid masses with downward reaching strands around the phloem represent what was termed an "inner sheath" by Renault (1879), Stopes (1903), Benson (1912), Lignier (1913) and others. Stopes describes the inner sheath of *C. principalis* as an arc of small, thick-walled, tracheid-like cells, located just inside the outer sheath, which enclosed the phloem and was attached to the flanks of the centripetal xylem where about 5 or 6 cells formed a group on either side. Such a description is identical to the condition found for the leaves in the present study, except that a complete arc around the phloem was only rarely observable. It is our opinion that the earlier interpretation of these lateral tracheids as an "inner sheath of primitive transfusion tissue" was an overzealous attempt to apply certain concepts of other gymnospermous foliage to what was then considered closely related cordaitean leaves. The terms "inner sheath" and "primitive transfusion tissue" would seem misleading, since the elements appear to be true xylem tracheids with scalariform or pitted markings. Even Stopes admitted that these inner sheath elements appeared much more like true xylem than the transfusion tissue of recent cycads. It, therefore, might seem a more logical interpretation to view these side elements simply as a flanking development of the centripetal xylem. This would result in a somewhat amphivasal condition developing in normally collateral bundles.

A striking feature of this species was the complete absence of centrifugal xylem in all leaf regions, although most other species reportedly had mesarch protoxylem giving rise to a mass of centripetal xylem above and

an arc of centrifugal xylem below. Reed and Sandoe assumed that their specimens had mesarch protoxylem, but failed to locate any protoxylem elements or to report the presence of any centrifugal xylem. This complete absence of centrifugal xylem conforms to Stopes' (1903) description of *C. principalis*.

Secondary xylem arranged in even radiating rows between the protoxylem and the phloem was observed in basal leaf portions, attesting to the existence of some cambial activity.

The phloem tissue was located below the protoxylem, but it was only rarely preserved. The elements in transverse sections were small, thin-walled, rectangular cells measuring 3–6×5–10 μ. They appeared badly crushed in longitudinal sections, and no sieve areas could be clearly identified.

The anatomy of the leaf base differed only slightly from other leaf portions. Paired leaf traces from the stem divided in several steps to form the 12–16 vascular bundles found at the base. These basal bundles were buried in the thick, uniform-appearing mesophyll, and did not contact the rather uniform layers of hypodermal sclerotic tissue (plate 125, fig. 6). At about 3 mm. from the base the vascular bundles began to dichotomize rather rapidly resulting in a high frequency of veins per cm. The hypodermal sclerotic ribs became more prominent, and as the leaf narrowed from the margins they began to make contact with the bundles. A slight evidence of lacunar tissue could be observed in the mesophyll at 5 mm. from the base. If considerable crushing of the basal 3 cm. of leaf had occurred, it often reduced the leaf thickness about 50% and obliterated the thin-walled cells composing the broad bundle sheath and compact mesophyll, resulting in the commonly found accordion-like leaf form illustrated in plate 125, fig. 1 which seemed to show an excessive amount of sclerotic tissue above and below the bundles. This leaf form was undoubtedly the one mentioned and illustrated by Baxter (1959) as belonging to his new terminal stem species of *Mesoxylon birame*.

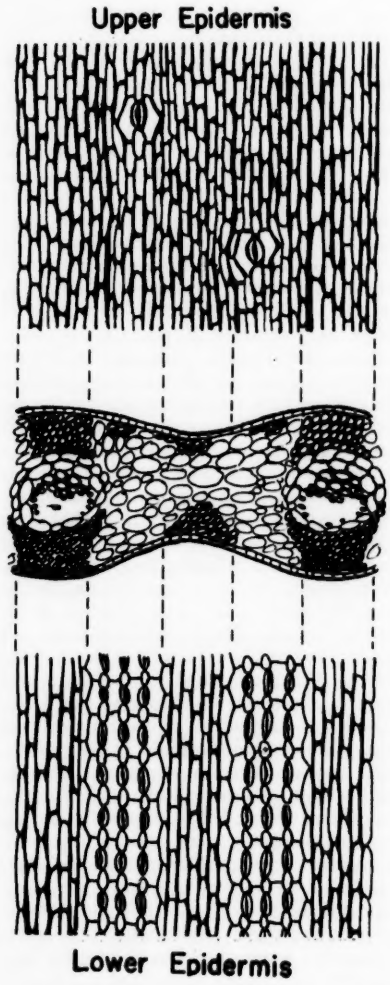
*Epidermal Structure.*—The lower epidermal structure, as seen in cuticles obtained from the maceration process and also sagittal sections, revealed the presence of stomatiferous bands alternating with nonstomatiferous bands of about equal width (plate 126, fig. 2). Although the width of these bands varied considerably, about 200 μ was average. The regular epidermal cells in the nonstomatiferous bands were elongated and rectilinearly arranged in a direction parallel to the veins. They were rectangular in shape, averaging 20–60 μ in surface dimensions and 30 μ in depth, but showing a great size variation from leaf to leaf and even on the same leaf.

The stomatiferous bands were composed of stomata arranged in linear rows, typically 3 in number, but often 2 or 4, and occasionally only 1 or as many as 5. These bands were located in the inter-rib regions, 2 between each pair of veins, as diagrammatically depicted in text-fig. 6. Oblique sagittal sections (plate 126, fig. 3) which progressively cut through the epidermal cells and then the underlying tissue, best revealed this correlation of the bands with the internal anatomy. The macerated cuticles themselves often gave good evidence of the position of these bands in relation to internal structure by the adherance of fibrous tissue.

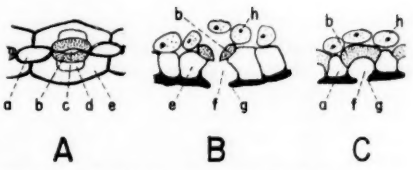
Each stomatal apparatus consisted of a pair of sunken guard cells surrounded by 2 lateral and 2 polar subsidiary cells (text-fig. 7; plate 126, fig. 6). The guard cells were small and crescent-shaped in surface view, oval in transverse section, and somewhat horseshoe-shaped in radial view, averaging about 10–15 μ in width and depth and 40 μ in length. The guard cells frequently appeared to contain granular contents as if indicating some cytoplasmic preservation. The angular bean-shaped lateral subsidiary cells were slightly wider than the normal epidermal cells, averaging 25×55 μ in surface view, and slightly smaller than Reed and Sandoe's measurements of 35×50 μ. The polar subsidiary cells were nearly elliptical in shape, with average dimensions agreeing exactly with Reed and Sandoe's 15×25 μ. If the stomata were not consecutive in a stomatal row the polar subsidiary cells were as long as 40 μ.

Cuticular extensions overhanging the stomatal openings were noted on both lateral and polar subsidiary cells in transverse and radial sections (text-fig. 6) forming the epistomal chambers previously reported by Reed and Sandoe. Sometimes

these cuticular extensions were pointed outward giving the appearance of papillae somewhat similar to, but considerably shorter than those reported by Florin (1931) for *C. lingulatus*. When the cuticles were observed in surface view somewhat of a sloping depression appeared on the inner side of each lateral subsidiary cell where it was attached to the guard cell. This circular hollow undoubtedly represents the same epistomal chamber as seen more readily in transverse and radial sections.




TEXT-FIG. 6—Correlation of epidermal patterns with internal anatomy for *Cordaites principalis*.




TEXT-FIG. 7—Various views of *Cordaites principalis* stomal apparatus. *A*—surface view, *B*—transverse section, *C*—radial section. *a*, polar subsidiary cell; *b*, guard cell; *c*, stoma; *d*, hollowed depression; *e*, lateral subsidiary cell; *f*, epistomal chamber; *g*,cuticular extensions overhanging epistomal chamber; *h*, mesophyll cell.

Usually a single row of lateral subsidiary cells was shared by 2 parallel rows of stomata, although frequently the stomatal rows were separated by several rows of normal epidermal cells. Typically, the stomata were arranged in continuous chains with a single polar subsidiary cell common to 2 consecutive stomata, but occasionally the arrangement was less regular with the stomatal chains broken more frequently toward the basal region of the leaf, where only rarely were more than 2 stomatal rows continuous for any great distance, although the third row could frequently be detected between them. The regular epidermal cells located within the stomatiferous bands were generally somewhat shorter than those of the nonstomatiferous bands. Within 5 mm. of the base the epidermal cells appeared strikingly shorter and almost isodiametrical, although still arranged in rectilinear rows. An average stomatal frequency of 124/mm.$^2$ was ascertained for the lower epidermis.

The epidermal pattern of the upper epidermis (plate 126, fig. 5) differed from that of the lower in the apparent absence of regularly alternating stomatiferous and nonstomatiferous bands. The epidermal cells appeared rather uniform and essentially like those of the nonstomatiferous bands of the lower epidermis except that they were somewhat deeper as seen in transverse and radial sections.

Stomata were definitely present, however, on the upper epidermis, contrary to the data

of Reed and Sandoe. These stomata were rather infrequent on the majority of specimens and usually appeared quite scattered, and in such cases it was difficult to observe any apparent pattern except that they occurred in the inter-rib regions (text-fig. 6). However, in a number of specimens, the stomata were far more numerous, and occurred in definite stomatal rows, although often quite separated within that row. Sometimes these stomatal rows were located within 2–5 epidermal cell rows of each other, with their arrangement strongly suggesting a basic similarity to the stomatiferous band arrangement of the lower epidermis. An average stomatal frequency of 6/mm.$^2$ was ascertained for the upper epidermis.

The stomatal apparatus on the upper epidermis was essentially like that of the lower epidermis except that the guard cells were more submerged, due to the greater depth of the subsidiary cells. The polar subsidiary cells, seldom connecting consecutive stomata, were not oval but elongated to about 40 $\mu$.

*Basis for Identification.*—This study has shown a striking resemblance between the species described as *C. affinis* by Reed and Sandoe from American coal balls and *C. principalis* anatomically described by Renault and Stopes from European petrifactions. In view of the great similarities between these 2 forms, it is deemed worthwhile to critically review the following criteria by which Reed and Sandoe have distinguished their species from *C. principalis:*

(1) Differences in leaf thickness,
(2) Differences in the distance between the bundles,
(3) The presence in *C. principalis* of intervening longitudinally elongated layers of cells in the central region between the bundles,
(4) The presence in *C. principalis* of an inner sheath of thick-walled "primitive transfusion tissue."

Leaf thickness is admittedly a poor criterion for classification as it is quite dependent upon vertical compression, but the present study revealed that non-basal leaf regions of the leaves in question varied from 0.3–0.5 mm. in thickness, agreeing very well with Stopes' report of 0.4 mm. as the leaf thickness of *C. principalis.* The distance between the bundles was not directly stated by Reed and Sandoe for their species, but it can be inferred from their measurements of leaf width and total number of veins, to average about 0.75 mm. In the present study, the average distance between the veins varied from 0.36–0.77 mm. Since the reported distances between the veins of *C. principalis* vary from 0.45–0.67 mm., this is scarcely a basis for differentiation.

Although Reed and Sandoe stated that their species differed fundamentally from *C. principalis* because of an absence of intervening elongated layers of cells extending between the bundles, sagittal sections in the present study clearly revealed such apparent strands of cells due to the previously described mesophyll plates being oriented in this direction. Even transverse sections of some considerably compressed leaves revealed apparent transversely extending strands, probably due to the mesophyll plates being obliquely slanted from crushing and seen in edge view. While the significance given to these transverse parenchyma chains by early workers, who sometimes interpreted them as possible "lateral transfusion tissue," was perhaps far-fetched, yet their presence in the mesophyll of both *C. principalis* and the leaves in question cannot be disputed.

Reed and Sandoe's contention that their leaves lacked the thick-walled inner sheath of "primitive transfusion tissue" possessed by *C. principalis* appears to be partly due to a difference in the interpretation of the lateral tracheids which extended downward either partially or completely around the phloem. While Reed and Sandoe illustrated some of these side tracheids as the downward extending points of their xylem arc, they did not identify them as part of the same tissue which Stopes perhaps misleadingly called an inner sheath of "primitive transfusion tissue." The present study has revealed these side "inner sheath" tracheids somewhat better developed than did Reed and Sandoe's figures, but still only rarely extending downward to form a complete arc around the phloem. In this respect the leaves in question seem somewhat unique, for both Renault and Stopes illustrated a complete arc around the phloem of *C. principalis.*

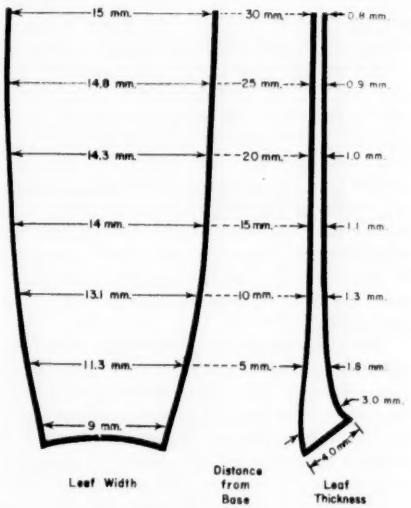
The single difference which exists be-

tween the leaves studied in the present research and the anatomical descriptions of *C. principalis* seems relatively minor, and it is highly questionable whether it is worthy of specific recognition. This view of the probable specific identity of these 2 leaf forms is enhanced by the occurrence of *C. principalis* as a common compression form in both North America and Europe, and the excellent agreement of morphological characters of these petrified specimens with those reported for compression specimens. The epithet, *Cordaites affinis* Reed and Sandoe, is, as previously stated, already illegitimate because it is a homonym. No new specific epithet is proposed to replace it, however, because it is our belief that this American anatomical form differs in no fundamental respect from the anatomical and morphological descriptions of *Cordaites principalis* (Germ.) Gein.

CORDAITES CRASSUS

*Occurrence.*—Coal balls from the Oskaloosa and Ottumwa, Iowa, area yielded large numbers of leaves that could be identified as belonging to *C. crassus* Renault. Darrah (1940, 1941) reported the species from this same area, as well as from the localities of Waukee, Urbandale and Williamson, Iowa. *C. crassus* leaves seemed conspicuously absent in all West Mineral and What Cheer coal balls where *C. principalis* was the dominating form. It was somewhat surprising that these 2 leaf species were not found associated except for a single *C. principalis* leaf found in Carbon Hill coal ball 1092 which otherwise contained numerous *C. crassus* leaves. The reason for this rather sharp distinction is not known, but it may have represented some local distribution difference, or perhaps might be better explained if the geological horizons of the coal measures involved were more exactly determined.

*External Morphology.*—*C. crassus* represents an anatomical species described only from petrifactions, with very little known of its external morphology. The coal ball specimens varied in total width from leaf bases of only 7 mm. to leaves as wide as 5.3 cm., but the majority seemed to range from 1.5–3.0 cm. The longest fragment observed just slightly exceeded 9 cm., but this is considered a mere fraction of the total leaf length, since the width changed only slightly in that distance.




TEXT-FIG. 8—Reconstruction of *Cordaites crassus* leaf base indicating changes in width and thickness with increasing distance from base.

The leaves were comparatively very thick and fleshy, lacking the exaggerated undulating form characteristic of many other cordaitean leaves. The thickness varied from only 0.1 mm. in some young leaves to as much as 3.5 mm. at some leaf bases, but the majority of the leaf sections encountered were in the 0.5–1.0 mm. range. Although neither Renault (1879) nor Darrah (1940) specifically reported the leaf thickness, it may be inferred from the magnification scales of their figures that Renault's specimen from French petrifactions was about 0.5 mm. while Darrah's specimen from Iowa coal balls was about 1.5 mm. in thickness, placing both well within the range of the present findings. The leaves all appeared thicker in the central regions and tapered toward the bluntly rounded margins which were only about 0.15 mm. in thickness.

The basal morphology has been carefully studied and diagrammatically reconstructed in text-fig. 8. The leaf base was much thickened and recurved, with a markedly concave

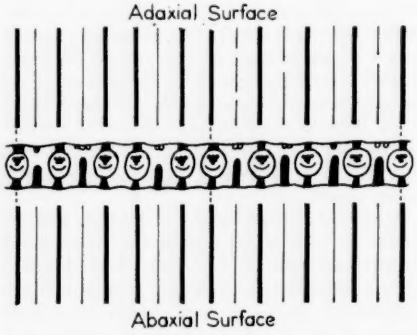
adaxial surface, and somewhat incurved margins (plate 127, fig. 1). From a basal width of 7–9 mm., the leaf initially widened rather sharply to a 12–15 mm. width during the first cm. upward from the base. Thereafter, the leaf increased in width only gradually at a scarcely observable rate. The leaf base thickness was about 2.0–3.5 mm. In the first 3 mm. upward the leaf thickness was reduced markedly by about 50%. The leaves then thinned steadily at a much reduced rate for about 3 cm., and thereafter, if the leaves did become progressively thinner, the process was so gradual as to be imperceptible.

The external surfaces were marked by the parallel ribbing characteristic of all cordaitean foliage. The ribs dichotomized frequently at very acute angles near the base, but less often upward. The surfaces were unusually smooth, with the ribbing sometimes scarcely visible without magnification, thus substantiating Renault's suggestion that the leaves of this species should show only slight relief. The primary external ribs generally marked the position of the internal veins and were separated by fairly prominent secondary ribs marking the position of the large intermediate sclerotic strands. A tremendous range of variation was observed in superficial ribbing patterns, largely reflecting the irregular spacing and great variability in the internal vein frequency, which ranged from only 15 to as many as 40 veins/cm. The distance between the veins ranged from 0.25–0.66 mm., which represents a somewhat shorter distance than Renault's reported 0.7 mm. distance but more in agreement with Darrah's distance of 0.4–1.0 mm. The younger leaves, identified as such from a comparison with the inner leaves of a bud, possessed the greatest vein frequency, often exceeding twice that of the older leaves. The average vein, and therefore primary superficial rib, frequency was about 26/cm., with the veins 0.38 mm. apart, but discounting the young leaf forms, it was only about 23/cm. with the veins 0.43 mm. distance apart. The primary ribs often appeared paired due to the paired nature of the internal veins which, at least near the base, dichotomized frequently and subsequently separated very slowly, continuing long distances before the large intermediate sclerotic strands developed between them producing secondary external ribs. This frequently paired nature of the veins was noted by Darrah who listed it as one of the characteristics of this species.

The ribbing pattern of the adaxial and abaxial surfaces appeared similar except that the intermediate ribs were generally more prominent on the abaxial surface. Often the large intermediate sclerotic strands on the abaxial side caused external ribs just as prominent as those associated with the veins, resulting in as many as 70 equal ribs/cm. The superficial ribbing pattern was still further complicated by the occasional occurrence of smaller internal sclerotic masses between the veins and the main intermediate sclerotic projections, causing fine superficial striae between the primary and secondary ribs (text-fig. 9).

It is disturbing to realize that if these leaves were to be found in impression or compression material, the same internal form might easily be relegated to at least 5, if not more, different species on the basis of different ribbing patterns. It is quite likely that just such situations account for the great abundance of described compression species, and points to the doubtful reliability of using external ribbing patterns in cordaitean leaf classification.

*Internal Anatomy.*—The most outstanding characteristic serving to identify *C. crassus* leaves was the extremely prominent abaxial hypodermal sclerotic masses project-




TEXT-FIG. 9—Correlation of adaxial and abaxial ribbing patterns with internal sclerotic masses in *Cordaites crassus*.

ing far into the mesophyll between the vascular bundles, often extending beyond half the leaf thickness. Nevertheless, the extent of the hypodermal sclerotic tissue in this species was highly variable. Sclerotic masses were located above and below the veins. Frequently these strands did not directly contact the bundle sheath, yet, contrary to the reports of Renault and Darrah, in the majority of cases these strands actually did abut against the bundle sheath. Occasionally there were additional smaller hypodermal sclerotic masses on both surfaces between the large intermediate ribs and those associated with the veins. The very fleshy leaf base (plate 127, fig. 1) had a more-or-less continuous hypodermal fiber layer, but none of the ribs projected inward as far as the veins. Beyond 3 mm. from the base, but still in the proximal region, there was considerable sclerotic development under both the abaxial and adaxial surfaces (plate 127, fig. 3), and a fairly prominent intermediate sclerotic rib was located between the veins on the adaxial side opposing a larger one on the abaxial side. At times these ribs joined to form a continuous fiber band from epidermis to epidermis between each pair or 2 pairs of veins (plate 127, fig. 4), similar to the condition reported for *C. felicis* by Benson (1912). Darrah (1940) reported that numerous Iowa coal balls contained leaves that appeared to be much closer to *C. felicis* than *C. crassus* and later (1941) definitely listed the former as being found in Iowa coal balls. However, the results of the present investigation seem to rather clearly indicate the specific identity of this form with *C. crassus*, as the transition was often shown in successive sections of the same leaf. Such a conclusion based on Iowa material may perhaps raise a question concerning the distinctness of the European forms of *C. felicis*, *C. weristeri*, and *C. crasus*, which differ only slightly except for their hypodermal sclerotic arrangement, but any such discussion is behond the scope of this paper. Beyond the proximal region, the amount of sclerotic tissue decreased gradually until the adaxial intermediate rib was entirely supplanted by a mass of very large, darkly colored, parenchyma cells (plate 128, fig. 1) to be discussed later in connection with the mesophyll.

The leaf margins, as in *C. principalis*, were supported by a considerable layer of hypodermal sclerotic tissue which undoubtedly helped to maintain uncrushed the blunt rounded edges in petrifactions. The individual elements of these sclerotic strands were typical fibers with oblique end walls tapering at about 45° angles. The cross-sectional diameters ranged from 5–20 $\mu$ but averaged about 15 $\mu$, while their length averaged about 0.45 mm. but occasionally reached 1.9 mm. The fiber walls were 2–5 $\mu$ in thickness.

The mesophyll was basically similar to that of *C. principalis*, but was slightly more compact and less lacunar. In mature, non-basal, non-marginal regions, the mesophyll was in the form of plates separated by lacunar slits. These frequently anastomosing plates were oriented in a direction perpendicular to both the veins and the laminar surfaces. In transverse leaf sections these plates were frequently revealed in face view giving a dense mesophyll appearance, while in radial sections (plate 127, fig. 5) and sagittal sections, these plates were intersected giving the appearance of anastomosing strands of parenchyma cells separated by lacunae, an appearance also reported by Renault in his description of this species. The plates were usually composed of about 11 cell rows extending between the adaxial and abaxial surfaces as seen in radial sections, and 6 cell rows extending from vein to vein as seen in sagittal sections, but this varied with leaf thickness and vein frequency. The plates, however, seldom extended from vein to vein, since they were interrupted by the large intermediate sclerotic strands. The lacunar slits near the adaxial surface narrowed making the upper mesophyll more compact than the lower, especially in younger leaves, but in general this species could hardiy be designated as having more than a very "incipient palisade" region. The mesophyll cells usually ranged from 20–40 $\mu$ in cross-sectional diameter, but were only about 15–25 $\mu$ in depth, giving the apperance of vertically elongated cells in radial sections and transversely elongated cells in sagittal sections.

An unusual feature observed in mature, non-basal leaf regions, was the aforementioned replacement of the adaxial sclerotic

rib by longitudinal rows of very large, isodiametrical, darkly stained, parenchyma cells about 40–70 μ in diameter, running parallel to the veins and perpendicular to the mesophyll plates. The transverse section of plate 128, fig. 1, the radial section of plate 127, fig. 5, and the sagittal section of plate 128, fig. 3 reveal these chains of large cells. The significance of this feature is not known.

The vascular bundles were rather large, usually occupying about 50%, but occasionally as much as 75%, of the leaf thickness. They were enclosed by a well-defined sheath of thin-walled cells which were elongated in the direction of the vein courses. The sheath cells were nearly isodiametrical in transverse view, but rectangular with straight end walls and arranged in even brick-like rows in longitudinal section. The sheath was as wide as 6 or 7 cell layers above, narrowing to only 2 or 3 rows on the sides, and widening again to 4 or 5 cell layers below. The outer layer of the sheath was often composed of very irregularly sized cells, with occasional large cells intermixed with smaller ones, and characteristically stained with dark opaque materials. The inner layers were generally composed of smaller elements. The sheath elements varied from 20–40 μ in diameter and 60–175 μ in length, and some possessed bordered pits.

Frequently, when the bundle sheath did not directly contact the inferior and superior hypodermal sclerotic masses, there occurred in the intervening region a modified type of tissue somewhat intermediate between the normal mesophyll parenchyma and the true bundle sheath elements. The cells of this tissue were somewhat elongated in the direction of the vein courses, but gradually intergraded with the normal mesophyll cells at either side. The significance of these cells is not clear, but perhaps they lend some credence to the theory that the bundle sheath, which Darrah (1940) described as of doubtful origin, may have been derived from the mesophyll.

The protoxylem, consisting of a few small spiral tracheids of about 4–7 μ in diameter, was located toward the central part of the bundle. It was mesarch, giving rise to a large-wedge shaped mass of centripetal xylem above and usually, in mature leaves, a narrow arc of centrifugal xylem below. The centripetal xylem was composed of small scalariform tracheids about 10–20 μ in diameter, and larger scalariform, reticulate, and pitted tracheids in the uppermost region of the bundle often reaching 45 μ in diameter. Some of the tracheids attained a length of 1.4 mm. as seen in longitudinal sections.

The centrifugal xylem usually consisted of a V-shaped arc of 1 or 2 rows of relatively small and generally reticulate-pitted tracheids of 8–20 μ in diameter. A row of small parenchyma cells separated the centrifugal xylem from the protoxylem and centripetal xylem. Often the upper ends of the centrifugal xylem arc were attached to the sides of the centripetal xylem mass. The presence or absence of centrifugal xylem was perhaps one of the most variable features of these leaves. It was consistently absent in young leaves, as might be expected, since Lignier (1913) reports it to have been the last vascular tissue to develop, and seldom present in bundles near the leaf margin. However, even in other regions, the centrifugal xylem arc was often absent for no accountable reason.

A small mass of tracheids frequently was present on either side of the wedge-shaped mass of centripetal xylem, somewhat similar to that described for *C. principalis*. Also a few small, scattered, thick-walled tracheids were occasionally found along the sides and beneath the phloem just within the bundle sheath, evidently representing a trace of what various early writers have termed the "inner sheath" in other species. However, these side tracheids were much less frequent in *C. crassus* than they were in *C. principalis* and could almost be disregarded as a normal occurrence. Renault (1879) indicated that this absence of an external vascular arc helped to characterize this species.

Considerable secondary xylem (plate 127, fig. 2) was frequently observed at the leaf base, located between the protoxylem and the phloem, and obscuring the centrifugal metaxylem if the later were ever present.

The phloem was located in the lower region of the bundle between the centrifugal xylem and the lower bundle sheath ele-

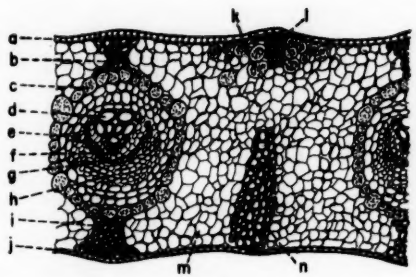
ments. Although the phloem cells usually had disintegrated prior to fossilization, in a surprising number of instances it was found remarkably well preserved. The phloem elements were oval-shaped with delicate, wavy-margined walls, varying from 4–10 $\mu$ in cross-sectional diameter. No sieve areas could be clearly identified in longitudinal sections.

Text-fig. 10 represents a labeled transverse section to help clarify the foregoing discussion.

*Epidermal structure.*—The regular epidermal cells of the abaxial surface were rectangular in shape, averaging $16 \times 18$ $\mu$ in surface dimensions, and 18 $\mu$ in depth, but showing great size variation on the same leaf as well as from leaf to leaf. They were aligned in regular lengthwise rows parallel to the sclerotic ribs and vein courses.

The stomata were arranged in definite stomatal rows, but the organization of these rows into stomatiferous bands differed considerably in various leaf parts. In basal leaf portions, having considerable sclerotic tissue, single or double stomatal rows were located in the regions between the veins and intermediate ribs (text-fig. 11). This formed a superficial epidermal pattern of rather evenly spaced stomatiferous bands separated by wider, fairly equal, nonstomatiferous bands. However, the frequent dichotomizing of the internal veins in the basal leaf regions often caused considerable variation in the width and frequency of the bands.

In non-basal leaf portions where the sclerotic tissue was much reduced, additional stomatal rows appeared to have been added on the side of the stomatiferous bands adjacent to the intermediate rib, eventually forming a very wide band of 5–8 stomatal rows (text-fig. 11). These wide bands occupied most of the inter-vein region, and were separated by nonstomatiferous bands of about half their width occurring at the vein regions (plate 128, fig. 4). It was this latter epidermal pattern that seems to have been described by Renault (1879), and redescribed by Seward and Sahni (1920), as a stomatal arrangement in 5 or 6 alternative rows. A close observation of the wide bands revealed that a band was actually separated into 2 parts by a very narrow nonstomatiferous strip of about 3 cell rows width lo-



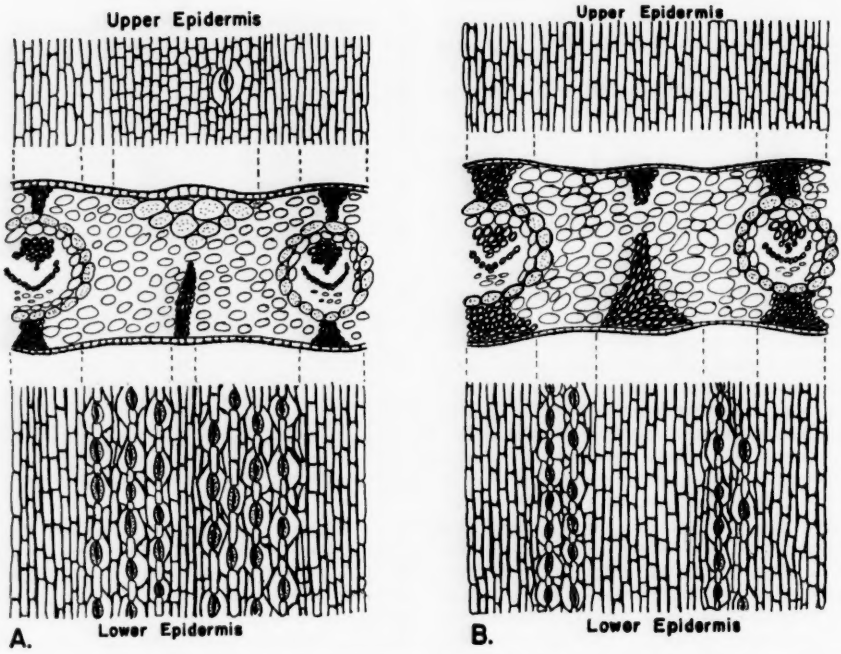

TEXT-FIG. *10*—Transverse section of *Cordaites crassus*. *a*, adaxial epidermis; *b*, superior hypodermal sclerotic strand above vein; *c*, bundle sheath; *d*, centripetal metaxylem; *e*, lateral tracheids or "inner sheath;" *f*, protoxylem; *g*, centrifugal metaxylem; *h*, phloem; *i*, inferior hypodermal sclerotic strand below vein; *j*, abaxial epidermis; *k*, large parenchyma cells replacing intermediate sclerotic strand on adaxial side; *l*, intermediate adaxial sclerotic strand; *m*, mesophyll; *n*, intermediate abaxial sclerotic strand.

cated immediately below the location of the intermediate sclerotic rib. The correlation of the lower epidermal pattern with the internal leaf anatomy was most clearly shown by oblique sagittal sections which first cut through the epidermal cells and then through the underlying tissues, but the adherence of fibrous tissue to the macerated cuticles also helped to reveal this relationship.

A frequently observed intermediate epidermal form between the basal and non-basal pattern had equal paired bands of about 3 stomatal rows resulting from the regular alternation of the stomatiferous bands with the wide nonstomatiferous bands of the vein regions and the narrower nonstomatiferous bands of the intermediate rib regions.

An average stomatal frequency of 164/mm.$^2$ was ascertained for the lower epidermis, comparing with Renault's figure of 150/mm.$^2$. This frequency was highly variable, however, ranging from 70–250/mm.$^2$ for different leaves.

Each stomatal apparatus consisted of a pair of sunken guard cells surrounded by 2 lateral and 2 polar subsidiary cells. The guard cells agreed almost exactly in size and shape with those of *C. principalis*. The lateral subsidiary cells frequently appeared




TEXT-FIG. 11—Correlation of epidermal patterns with internal anatomy for *Cordaites crassus*. *A*—non-proximal region, *B*—proximal region.

rather unequal in size and shape, but were generally somewhat longer and broader than the regular epidermal cells, averaging 20 $\times$65 $\mu$ in surface dimensions. The polar subsidiary cells, averaging 17$\times$30 $\mu$ in surface view, were not nearly as ovoid in their appearance as were those of *C. principalis*, a fact partially explained by their less frequently serving to connect consecutive stomata. Small cuticular extensions overhung the stomal region forming an epistomal chamber above the guard cells similar to that of *C. principalis*. Otherwise, there were no epidermal hairs, papillae or cuticular appendages of any kind, this being in agreement with the previous descriptions of Renault (1879) and Seward and Sahni (1920).

The typical epidermal cells of the upper surface were essentially similar to those of the nonstomatiferous bands of the lower epidermis, averaging 19$\times$65 $\mu$ in surface view and 21 $\mu$ in depth. An unusual banded appearance (text-fig. 11; plate 128, fig. 2) characterized some regions of the upper epidermis, which was caused by alternating strips of different cell shapes. This banded pattern was observed in regions containing the intermediate strands of large parenchyma cells. The epidermal cells just above this specialized parenchymatous tissue differed markedly by being shorter, broader, and deeper. The correlation between the internal masses of large parenchyma cells and the difference in epidermal cell shape can be noted even in transverse sections but is most clearly revealed in oblique sagittal sections (plate 128, fig. 3).

Contrary to the reports of Renault (1879) and Seward and Sahni (1920), stomata were definitely present on the upper epidermis but were extremely rare, with an average frequency of approximately 1/mm.$^2$. They were found in the inter-vein regions usually

located in the specialized bands of shorter, thicker epidermal cells, and were essentially similar in structure to those of the lower epidermis except that the guard cells were more deeply recessed below the surface. The cuticular extensions of the subsidiary cells were also somewhat more pronounced, probably due to the presence of a thicker layer of cutin on the upper epidermis.

### KEY TO CORDAITES ANATOMICAL LEAF SPECIES

The following key, based on anatomical features, is presented as an aid in identification of *Cordaites* leaf species which have been so described.

A. Veins unequal in size with large central bundles alternating with smaller bundles appearing only on abaxial side ..... *C. duplicinervis* Gr.'Eury

A. Veins equal in size

B. Exarch xylem arrangement; triangular wedge of metaxylem tracheids radiating upward from a protoxylem area at its lowest point.

C. Hypodermal sclerotic tissue apparently limited to triangular masses above and below the veins

D. Mesophyll not differentiated into a definite palisade and spongy region ..... *C. rotundinervis* Gr.'Eury

D. Mesophyll differentiated into definite palisade and spongy region

E. Upper epidermal cells not bearing papillae; approximately 25 veins/cm ..... *C. rhombinervis* Gr.'Eury

E. Upper epidermal cells bearing papillae; approximately 17 veins/cm ..... *C. tenuistriatus* Gr.'Eury

C. Hypodermal sclerotic tissue not limited to vein regions, consisting of rather prominent abaxial masses about midway between the veins and about 3 (0–5) much smaller irregular intermediate adaxial masses, in addition to triangular masses above and below the veins ..... *C. principalis* (Germ.) Gein.

B. Mesarch xylem arrangement; a large superior mass of centripetal metaxylem tracheids radiating upward from a protoxylem point, and a narrow crescent of centrifugal metaxylem tracheids inferior to the protoxylem.

F. Hypodermal sclerotic tissue limited to triangular masses above and below the veins; mesophyll differentiated into palisade and spongy region; papillae on lower epidermal cells ..... *C. lingulatus* Gr.'Eury

F. Hypodermal sclerotic tissue not limited to vein regions; mesophyll not clearly differentiated into palisade and spongy region, although more compact near the adaxial side; papillae not present on lower epidermal cells.

G. Intermediate sclerotic strand extending completely across the leaf midway between the veins ..... *C. felicis* Benson

G. Intermediate sclerotic strands not extending completely across the leaf (excepting some portions of *C. crassus*)

H. Very large intermediate sclerotic masses, most extending more than halfway across the leaf from the abaxial side ..... *C. crassus* Renault

H. Intermediate abaxial sclerotic ribs never extending more than halfway across the leaf.

I. Well-developed hypodermal sclerotic masses above and below veins always abutting to bundle sheath, veins large, about 17/cm.; sclerotic bundle sheath ..... *C. angulosostriatus* Gr.'Eury

I. Small hypodermal sclerotic masses above and below veins often not abutting to bundle sheath; veins small, about 26/cm.; bundle sheath not sclerotic ..... *C. weristeri* Leclercq

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# NEO-LAMARCKISM, MODERN DARWINISM, AND THE ORIGIN OF THE VERTEBRATES*

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ABSTRACT—The annelid—prot-arthropod ancestry of the vertebrates has recently been asserted on a Lamarckian basis. Lamarckism and modern Darwinism are here contrasted, and it is shown that the current neo-Lamarckian criticisms of the current theory of evolution are not valid. The current theory, of which mutation and natural selection are the most important parts, appears to be adequate to account for the observed results of evolution. Some of the major bases of the annelid prot-arthropod theory are then examined and shown to be erroneous. Finally, the Dipleurula theory of Bather is tentatively reasserted and shown to be the most satisfactory theory of the origin of the chordates in the present state of knowledge. Darwinian processes are adequate to achieve the necessary transition. The memory of Lamarck would be better served by reference to his many sound works than by the resuscitation of his greatest mistakes, his ideas on heredity and evolution.

## INTRODUCTION

IT WAS very much a surprise to find the annelid-arthropod ancestry of the vertebrates defended recently (Raw, 1960), and that, with no new fossil evidence to support it, in the Journal of Paleontology! That the author found it necessary to appeal to Lamarckism to support his claim is not surprising. Nor is he alone, for numerous neo-Lamarckian publications have appeared recently (Cannon, 1958; Cameron, 1958; Martin, 1953, 1956; Waddington, 1952). These men and their fellow neo-Lamarckians comprise a very small minority among zoologists today; nonetheless, they are highly competent and respected men in their several fields of specialization, and it is important to evaluate their criticisms of current evolutionary theory.

## THE THEORIES DEFINED

First, the Lamarckian and modern theories of evolution may be contrasted. Lamarckism is based upon four principles. First, living organisms and their component parts tend to increase in size. Second, new organs result from new needs and from the movements which these needs cause. Third, use of an organ results in its further development, whereas disuse results in its degeneration. Finally, modifications produced by the actions of these principles during the lifetime of an individual are inherited by the offspring, and their cumulative effects over long periods of time are responsible for the origin of species and higher groups. In a word, Lamarckism is the proposition that organisms respond to their environment purposefully by the formation of modifications which are adaptive to that environment.

Classical Darwinism maintained that the prodigality of nature and the relative restriction of adult populations require that there be a severe struggle for the means of life. And because all species of organisms vary, this can only lead to natural selection of those variants which are best fitted to their conditions of life and hence to the gradual modification of species (Darwin, 1859; Dodson, 1960).

In the main, the current theory accepts classical Darwinism, but where Darwin said that the fundamental laws of heredity are largely unknown, today Mendelian heredity is generally accepted as a necessary complement to Darwinism. The variability which Darwin observed to be a universal characteristic of natural species is now interpreted in terms of the various gene mutations which occur in every wild population. These are subject to Darwinian natural selection. The typical species, however, is widely distributed, and the selective factors in different parts of its range are quite unlike, hence selection leads to geographi-

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cally replacing subspecies, each with a typical constellation of gene frequencies. The continued action of the same forces may then lead to further divergence and formation of distinct species. Mutation and selection thus emerge as the major factors in evolution, while population structure and geographic distribution are important secondary factors.

## NEO-LAMARCKIAN CRITICISMS

The great appeal of Lamarckism derives from the observation of the universality of the fact of adaptation in nature. No species can long survive unless it is reasonably well adapted to its conditions of life. The Lamarckian inference that it is the conditions of life (i.e., the environment) which *produces* the adaptation is most alluring. Because Darwinians deny this, the neo-Lamarckians believe that they underestimate the importance of the environment (Raw, 1960). Actually, the environment is of fundamental importance for Darwinian evolution, for it is the environment with acts as *selector*, determining which of the random variants of a species shall increase in abundance and, hence, determine the future characteristics of the species. For Lamarckism, the environment *produces* variations which are, in fact, adaptational. For Darwinism, the environment selects adaptational mutations from a wide variety which exist in most wild species. Such a difference of interpretation would be unresolvable if there were no further evidence. Many studies, however, show that mutation occurs continually in all species, and that the great majority of these are deleterious (Babcock, 1947; Dobzhansky, 1951; Dodson 1960). Hence the observed facts accord with the Darwinian explanation.

A more serious criticism claims that nuclear (i.e., Mendelian) heredity is concerned only with trivial traits at the end of development, while the major features of the organism are determined by the cytoplasm and do not follow the principles of Mendelism. E. B. Wilson (1925) and Theodor Boveri set out to prove this proposition more than 60 years ago, but their experiments led to a conclusion diametrically opposed: that is, they concluded that heredity is almost entirely nuclear, with the cytoplasm functioning principally as a substrate for the action of the nucleus. Two of Boveri's (1896, 1902) experiments may be cited. In one, sea urchin eggs were broken into fragments by forcing them through a fine silk mesh. Some of the fragments included the maternal nucleus, while others were anuclear. These fragments were then fertilized by sperm of another species with distinctive larval morphology. The diploid zygotes, with a nucleus from each parent, showed a mixture of traits of both parental species. Yet haploid eggs showed almost exclusively paternal characteristics. As the cytoplasm is almost entirely maternal, the difference must be due to the nuclear component.

In a second experiment, Boveri found that sea urchin eggs, when exposed to a heavy suspension of sperm, were commonly fertilized by *two* sperm simultaneously. As a result, a tetrapolar division figure is established, and the zygote divides at once into four blastomeres. As the zygote includes three haploid sets of chromosomes, these are distributed at random among the four spindles, and hence some of the daughter cells are quite deficient, others have many extra chromosomes, and only occasionally will a blastomere get a normal diploid set of chromosomes. Only the last group of blastomeres developed normally, while all of the others developed abnormally or not all. Yet the cytoplasmic components of these cells are, on the average, the same.

It was, then, demonstrated long ago that nuclear heredity is not a mere gilding of the cytoplasmic lily. Modern studies have carried this very much further, for studies in physiological genetics have shown that cytoplasmic heredity may not be autonomous, but rather it is dependent upon nuclear genes. The clearest example is that of the killer factor in *Paramecium* (Sonneborn, 1947). Killer strains of this protozoan release a substance which kills sensitive strains. Crosses between the strains show that the killer trait depends upon a single dominant gene. Yet *Paramecia* with this gene are killers only if they also have a cytoplasmic factor, kappa. Kappa can be maintained only in the presence of K, and K expresses its phenotype only through kappa. Some physiological geneticists believe that collaboration of such pairs of nuclear genes

and plasma genes is the ordinary mode of genic action.

In terms of the genetics of 1920, there was some justification for the statement that Mendelian genetics was concerned only with trivial traits added at the end of development. Mutants are now known, however, with principle effects at *every* stage of the life cycle. Let us consider especially the lethal genes, a class of genes which cannot be considered as trivial, for they influence vital processes decisively. The first example to be well studied was yellow coat color in mice (Cuénot, 1902). This gene is lethal when homozygous, and it was shown that the homozygous embryos are actually visibly abnormal as early as the morula stage. In Hadorn's (1951) study of lethality in *Dorsophila*, genes were demonstrated with effects at every stage in the life cycle from the zygote to the adult.

Perhaps the experimental embryologists have discovered nothlng more fundamental than the primary organizer of the chordates, which is invaginated during gastrulation and plays a leading role in the formation of the central nervous system and of the primary germ layers. In mice there is a whole family of mutant genes which lead to defects of the spine, gait, or balance. Some are lethal when homozygous. These appear to act through modification of the primary organizer.

Another system of related mutations is the achondroplastic type. This is well known in many mammals as an abnormality characterized by deficient development of the long bones. It is based upon a dominant gene which is lethal when homozygous in cattle, chickens, and probably man. Yet a similar mutation, with unimpaired viability, is responsible for the bulldog type of dogs. The developmental aspects of this gene have been thoroughly studied in chickens by Landauer (1934). Heterozygotes are not markedly abnormal except for the retarded development of the replacement bones. The homozygotes, however, are grossly abnormal even in very early stages. As development proceeds, not only the skeletal system but also the circulatory system is defective. It has even been suggested that all mesodermal derivatives are affected.

Perhaps these examples are sufficient to establish the point that nuclear heredity is not confined to trivial traits at the end of development. Actually, nuclear heredity has been demonstrated to be effective at every stage of the life cycle.

Another source of neo-Lamarckian skepticism is the erroneous impression, quite common among non-geneticists, that mutation is a very rare phenomenon, too rare to be an important factor in evolution (see below). To this, Martin (1953) adds that most mutations are injurious to the organism, and, while he regards this as extremely important, he believes that most geneticists know it but consider it unimportant. It is certainly true that most mutations are deleterious, but geneticists consider this to be *highly* important: it is one of the major bases of the concept that mutation is a *random* phenomenon with respect to adaptive value. If this is correct, then advantageous mutations ought to be rare relative to deleterious ones. On the other hand, if mutations were *directed* toward advantageous end products, observed mutation rates should lead to very rapid evolution indeed.

Martin is impressed by the fact that artificial mutagens, such as radiation and nitrogen mustard, are injurious agents, and he believes that naturally occurring mutations must also be caused by injurious agents. He does not believe that injury can be a sound basis for knowledge. The causes of mutation in nature are not well understood, but even if Martin should be proven right regarding their injurious character, it would still not disprove the importance of mutation. Experimental mutation shares with almost all biological experimentation the use of techniques which are injurious to the organisms studied. If experimentally gained knowledge is to be respected only when the experiment has done no injury to the organism studied, we shall have to reject almost all of our experimentally gained knowledge in the biological sciences.

With respect to the multitude of normal genic differences in all natural species, Martin considers that "there is no evidence that they arose by mutation" as they are not pathological, and so they probably arose by Lamarckian modification. Many attempts have been made to verify Lamarckian origin of hereditary variations, but all have either

given equivocal results or have failed outright (Agar, 1954). Most impressive is the lack of result from thousands of years of circumcision of Jewish boys. It may be objected that this is an injury and so should produce mutations rather than Lamarckian effects. With respect to use and disuse, however, it is obvious these boys have not had the use of their prepuces. According to Lamarckian theory, the structure should have degenerated, yet no reduction has occurred. On the other hand, it has been conclusively proven many times that genetic changes actually are produced by means of mutation, i.e., a sudden change in the nature of a gene (Goldschmidt, 1955; Muller, 1952; Stadler, 1954). Hence it is reasonable for geneticists to attribute the origin of naturally occurring alleles to mutation until some definite evidence in favor of another mode of origin can be adduced.

The neo-Lamarckians are peculiarly split with respect to the Biogenetic Law, the old idea that "Ontogeny recapitulates phylogeny," the development of the individual being a condensed version of its ancestral history. Raw (1960) dismisses it with the statement that evolution has followed too long and complex a course to be represented in ontogeny. To paraphrase, the embryology of the vertebrates shows no features which are readily interpretable terms of annelid-arthropod ancestry. Yet he uses this "law" quite facilely when it serves his purpose. Martin (1953), however, is very favorably disposed toward the biogenetic law, regarding its validity as inconsistent with the proposition that mutations could affect any but the late stages in development, for, if hereditary changes were effective in early stages of development, all traces of parallelism would be lost. Hence, he concludes that mutations cannot have been important in evolution. He acknowledges that only the vertebrates exemplify this "law" at all well, but he believes that other phyla "completed the main part of their evolution so many millions of years ago that the principle of tachygenesis has condensed comparable stages of their development into too brief a period." The known history of the vertebrates extends back nearly half a billion years and they may have existed much longer—Raw would say *very* much longer—so that tachygenesis may have had quite sufficient time to operate in the chordates too. Appeal to such phenomena is gratuitous: it would be just as reasonable to assume that other phyla are typical with respect to their embryological diversity, while the chordates are atypical, perhaps because of that disruptive phenomenon, mutation!

Martin believes that geneticists have attacked the biogenetic law because it is anti-genetic, yet it has not been geneticists but embryologists who have led this attack. See, for example, the excellent paper of H. Barraclough Fell (1948). This attack began before the rise of modern genetics. Bateson (1922), who was an embryologist long before he became a geneticist, said that the morphologists of the latter half of the nineteenth century worked under the complete domination of the biogenetic law and that "Discussions of evolution came to an end primarily because it was obvious that no progress was being made." The *coup de grace* has been added by De Beer (1958), who has shown that embryological changes have been intercalated at all stages of vertebrate development.

Another neo-Lamarckian criticism is that the current theory cannot account for non-adaptive or mal-adaptive characters. Actually, there are quite a number of mechanisms by which this may be achieved, such as pleiotropic genes with other effects which are useful, close linkage to favored genes, or fixation by drift. Or the trait may have been valuable in the past, although it is now vestigial. Finally, a character may owe its selective value to its occasional use in extreme conditions. Thus, an extraordinary variety of plants is grown successfully in the benign climate of the San Francisco Bay region. Very rarely, however, freezing weather does strike and does great damage, but native plants fare better than do introduced plants. The characters which adapt the native plants to these extremes seem inexplicable in ordinary years, but like all insurance, the value is most apparent when needed.

However, the most important aspect of the non-adaptive characters is one which eludes the neo-Lamarckians: such characters present a much greater difficulty for La-

marckian theory. For, if the characters of organisms result from direct environmental induction of appropriate changes, *then all of the characters of any organism ought to be adaptive*, except for a time lag between a significant change in the environment and the induction of the appropriate changes.

These, then, are some of the more important criticisms which the neo-Lamarckians are directing against the current mutation-selection theory of evolution. They do not stand cross-examination, for they are based largely upon misunderstanding and outdated information.

### THE MUTATION-SELECTION THEORY AMPLIFIED

Let us now restate and amplify the current position of geneticists with respect to evolution. The first of the major problems of evolution is the origin of inheritable variability. There are only two demonstrated sources of such variability, and these are gene mutation and chromosomal mutation. One of the sources of neo-Lamarckian skepticism is the low frequency of mutation. Biologists who have not thought through the consequences of the ordinary mutation rates are inclined to doubt that so rare a phenomenon could provide a basis for the enormous range of diversity which is the end product of evolution. A detailed example may therefore be profitable. Mutation occurs at an average rate of 1/100,000 gametes per gene. Let us estimate that a typical vertebrate such as a salmon has 20,000 pairs of genes. Each of these has its own probability of mutation, and their separate probabilities may be added to get the collective probability that *some* gene will mutate. The result is an overall probability of 1 in 5 that any particular gamete will carry some new mutation. Now a codfish spawns in excess of 10,000,000 eggs, and so about 2,000,000 of these may be expected to carry one or more newly mutated genes. Now let us add the plausible but gratuitous assumption that only 1 mutation in 10,000 is potentially valuable to the species. This would still mean that in the spawn of a single codfish there would be as many as 200 eggs in which mutation had produced alleles of value to the species in its evolution—that is in its continual adaptation to the changing conditions of life. It *is* plausible, then, that even so slow a process as mutation may produce enough hereditary variability to meet the requirements of evolution.

Once the variant genes have been formed by mutation, they are reshuffled into new combinations by the mechanism of sexual reproduction. Most of these mutants are more or less abnormal, and their prospective fate is elimination by natural selection. But that occasional mutant which has adaptive value in the complex conditions of life will tend to spread in its population. Thus, the species tends always to approach a state of adaptation to its ever changing conditions of life. A typical species, however, is distributed over a wide area, embracing quite different conditions. Thus the deer mouse, *Peromyscus maniculatus* is distributed over most of the United States and considerable parts of Canada and Mexico. In this enormous area, some populations live in mountains and others on prairies. Some live on the shores of the Great Lakes, and others in the deserts of the Southwest. Some must adapt to the rigors of the Canadian winter, and others never know frost. It is obvious that the characteristics which adapt the species to such different habitats must be quite unlike. Hence natural selection will favor different genes in the different regions, and so recognizable geographic races, the subspecies, are formed.

Even the subspecies, however, may be widely distributed and very numerous. Each is, however, restricted by its ecological requirements to limited areas within its total range. The result is a checkerboard of moderate sized mouse communities, ranging up to a few thousand mice. These are the real breeding populations, within which there is free exchange of genes. A considerable, but more limited, exchange of genes occurs among the local populations of a subspecies because of occasional migration of individuals. Finally, wherever subspecies meet, there is a certain amount of interbreeding. The mathematical studies of Wright (1950) and others indicate that this type of population structure, which is typical in nature, is also optimal for the effectiveness of natural selection.

This process has been tested experimen-

tally and has been verified. The assumption that the same processes, continued over long reaches of time, would produce the more profound differentiation of species, genera, and higher categories is most attractive, but it is unproved. Whether this assumption is valid has been a hotly controversial question.

Part of the basis of this controversy is the lingering suspicion that our critics may be partly right when they doubt that mutation and selection can act rapidly enough to produce the observed results of evolution, even in the great extent of geological time. A number of mechanisms have been proposed which might accelerate the process. The most disputed of these is Goldschmidt's (1955) suggestion of *systemic mutations*, which would have their primary effects on early embryonic processes, thus leading to profound modification of the resultant adult. Goldschmidt believed that one or a few such mutations might form a new species rapidly. This would then be put to the test of natural selection at once, and, if successful, it would then be modified and diversified by the slower process described above. Again, Wright (1943) has suggested that, if selection pressure and predominant direction of mutation should happen to coincide, it might result in considerable acceleration of evolution. Also, major steps in evolution may be aided by strong selection pressures. For example, when Devonian fishes first invaded the land and gave rise to the Amphibia, they no doubt were rather poorly adapted to life on land, and considerably less well adapted to life in water than were their less progressive cousins. An enormous selective pressure must have favored either completion of the transition or return to the water. Again, when related species compete with each other in the same area, they often become much more strongly divergent than are the same species in areas where they occur separately. It is evident that selection favors differentiation because it places them in different ecological niches, thus reducing competition. To put it another way, differentiation of related populations allows a greater total number of individuals to survive in the same area. Brown & Wilson (1956) have studied this phenomenon extensively, and they call it character displacement. It is probable that some or all of these accelerating mechanisms are frequently effective.

## THE ANNELID—PROT-ARTHROPOD THEORY OF THE ORIGIN OF THE VERTEBRATES

Raw's derivation of the vertebrates from the annelids via the prot-arthropods is rather more fortunate than his espousal of Lamarckism. Although the present writer regards his argument as fundamentally wrong, he has assembled a great mass of data and his use of them in conjunction with the perennial problem of our own ancestry should stimulate many zoologists to reexamine their own thinking on this problem. He believes that many characteristics of primitive vertebrates are best understood in terms of derivation from a primitive polychaete annelid. These include the forebrain and nerve cord(s), segmental nerves, visceral nervous system, eyes, profuse segmentation, anlagen of the limbs, gills, and ciliated body surface.

He worked out a phylogeny of the prot-arthropods, based upon various primitive polychaetes and adult and larval trilobites, which is highly interesting and at least as probable as any other which has been published. Certain features of the primitive vertebrates he considers to be understandable only on the assumption that the vertebrates passed through the prot-arthropod stage. These include the gill arches and gill slits, the similarity of the heads of cephalaspids and of trilobites, the ventral position of the mouth, and the nature of the gut of the vertebrates.

A detailed discussion of Raw's argument would require an excessively long paper. Some of the more striking points, however, will be discussed below. That profuse segmentation is a prominent characteristic of the annelids and trilobites is beyond doubt. It also seems to have characterized the ostracoderms. While the segmentation of most modern fishes is still extensive, it is relatively reduced in the more specialized ones. Finally, segmentation is still an important characteristic of the tetrapods, even though it is obscured in many respects. Raw, thus, considers profuse segmentation to be a primitive vertebrate character most

easily explained as an inheritance from a profusely segmented ancestor, a prot-arthropod which is in turn derived from an annelid. The point is well taken, but plainly requires corroboration by specific homologies, or by other compelling means. Before examining that aspect, other possible explanations for profuse segmentation should be considered. Raw did consider Young's (1950) theory that it arose because of the adaptive value, for a swimmer, of subdividion of the longitudinal musculature into segments which could contract in series. He rejects it, because the earliest known fishes are already profusely segmented. Yet eleswhere he emphasizes that the earliest known fishes had already had an immensely long history, long enough to account for features which do not otherwise readily fit his theory. Quite possibly the ostracoderms were profusely segmented because they were the product of a long evolution during which an originally moderately segmented ancestor, possibly of the Dipleurula type, was subjected to selection for increasing segmentation because of its adaptive value for an active swimmer.

Like Gaskell and Patten before him, Raw is much impressed by the similarity of the heads of trilobites and ostracoderms. That there is a superficial resemblance is universally conceded: that there is any actual morphological homology is unproven and improbable. Raw points out that Stensio has identified 6 cranial nerves (by their foramina in the head shield) which innervated the lateral sensory areas of the cephalaspid head, and he suggests an homology to the 6 dorsal segments of the trilobite head. Yet there is nothing except coincidence of number to support the alleged homology—no morphological evidence whatever. His statement that the distribution of arteries and veins in the cephalaspid supports the homology is rendered absurd by the complete lack of knowledge of the internal anatomy of the trilobites. Future knowledge may vindicate his statement, but present knowledge cannot. Such reasoning recalls a statement attributed to Gauss that "I have had my results for a long time; but do not know yet how I am to arrive at them." It should also be mentioned that there is no evidence of homology of chitin and bone, nor of any transition from one to the other.

The history of the digestive tract is particularly interesting in Raw's theory. The annelids and prot-arthropods had a well developed digestive system which was essentially an entodermal tube running the length of the body. Because of the bottom feeding habit of the prot-arthropod, the mouth was shifted ventrally, and the prostomium was retroverted to form the labrum. The anterior-most appendages then served especially for the handling of food. When swimming by lateral undulations, all of the appendages were held close to the body, flexed at the middle, and meeting on the ventral mid-line, so as to present minimal interference with the undulating movement. They gradually fused to form a new ventral body wall, and to form a "food basket" which was open at both ends (because the prot-arthropod had a pair of appendages on every segment of the body). This formed a sort of sieve for concentration of food particles. At first, the food so obtained was passed forward to the mouth. Later, as increasing speed of swimming made it less practical to pass the food forward, the food basket acquired digestive cells and gradually became a secondary gut, while the original digestive system atrophied.

The mouth and anus are therefore the terminal openings of this secondary gut. Because of the increasing use of the tail as a propeller and rudder, however, the anus shifted forward. Raw believes that this is the explanation for the post-anal gut of vertebrate embryos.

The wall of the new gut was, thus, also the ventral body wall. Their separation by the coelom was accomplished by coelomic buds expanding into each appendage-component of the new gut, then expanding and fusing, leaving a continuous gut inside a continuous body wall, with a coelom separating the two.

Of the numerous difficulties which Raw has disregarded, a few may be mentioned. A system derived in the fashion described should be a prominently *segmented* system, yet, apart from the pharynx (which will be discussed below), the digestive system of vertebrates is perhaps their most unsegmented system. Further, there are no struc-

tures, either of the vertebrate gut or body wall, which even remotely suggest derivation from chitin encased, jointed appendages, such as the prot-arthropod must have had. In short, not only are there no specific homologies, but the basic plan of the vertebrate digestive system (and body wall) is quite different from that expected under Raw's system.

Raw attaches considerable importance to his explanation of the post-anal gut of vertebrate embryos. While it must be conceded that his explanation of the original terminal position of the anus is internally consistent with his own theory, still that is the usual position of the anus in many groups of invertebrates quite unrelated to the articulates. Once the full-length gut is established, if the use of the tail as a powerful propeller and rudder should favor anterior displacement of the anus, it is difficult to see why such a selective force would work any more readily upon a gut of appendicular-ectodermal origin than upon one of the more usual entodermal origin. Also, it is difficult to see why so trivial an aspect of the evolution of the gut should be accurately reflected in the embryology of all vertebrates, while its fundamental aspects (appendicular-ectodermal origin) are completely suppressed. It is far simpler and more logical to conclude that there is no evidence of the appendicular-ectodermal origin because it is an erroneous inference from misconstrued data.

The pharynx, with the gills and associated structures, requires special comment. It is in this region especially that Raw sees evidence of the appendicular-ectodermal origin of the digestive system, for to him the gill arches are simply arthropod appendages. and the gill slits are the spaces between consecutive appendages. Their respiratory function is easily explained, as each appendage of the prot-arthropod presumably bore an external gill. The respiratory epithelium need only migrate onto the surface of the gill arch and the vertebrate pharyngeal apparatus is complete.

The typical prot-arthropod appendage, as seen in the trilobites, is a *biramous* appendage, with a proximal protopodite followed by parallel endopodite and exopodite. Nothing comparable can be seen in the gill arches of any vertebrate. The series of segments of the arches of fishes, however, Raw suggests may be homologous with the series of joints in a typical arthropod appendage, but no specific homologies could be identified. Raw's entire argument ignores the fact that an arthropod limb is essentially a jointed cylinder of chitin containing muscles, nerves, and blood vessels, while the gill arches of vertebrates consist of a core of cartilage or bone surrounded by the fleshy components. Different materials are used in different ways, therefore there is no evidence of homology.

The problem of the fate of the original gut is an interesting one. Raw thinks that the hypophysis may be a remnant of it, a gland which has been adapted to new functions. For the rest, he believes that is has disappeared without a trace, a rather remarkable fate for a complex and extensive organ system.

Raw's discussion of other organ systems is quite comparable to those already discussed and will not be analyzed here. However, his evaluation of the significance of Amphioxus and other lower chordates should be alluded to, especially as his strongest point is here. This is the fact that Amphioxus which he regards as the most primitive chordate, has annelid-type nephridia, which are, in fact, very simular to those of the polychaete *Phyllodoce parretti*. When he says that "Since *Amphioxus* (sic!) still possesses annelid nephridia, it must have inherited them from the polychaete through the prot-arthropod" he has made a very strong point, but not strong enough to carry the argument in the absence of support from other organs and systems.

Raw believes that the proto-chordates have been kept primitive by early degeneration. He attaches great significance to Amphioxus because of its nephridia, because its extensive pharynx suggests to him the hypothetical food basket made up of prot-arthropod appendages, and because of certain other features which he interprets (I believe, incorrectly) in terms of his theory.

The tunicates he disposes of very quickly: "they are so degenerate that they need hardly be considered here." This is a remarkable statement in view of his earlier

statement in regard to the hypochord (a degenerate vestige underlying the notochord) that "most vestiges are keys to morphological problems." The hemichordates are not even mentioned. Collectively, he regards the lower chordates as so obviously degenerate that they ought not be considered in naming the phylum, and he considers that the name should be Vertebrata rather than Chordata. While it is true that the lower chordates are generally degenerate, there is no evidence that they have degenerated from a vertebrate stage, and so the more usual name of the phylum, Chordata, should be retained.

### THE PLACE OF THE CHORDATA IN THE ANIMAL KINGDOM

Quite apart from the defects of the annelid—prot-arthropod—chordate theory (Raw treats the three phyla as a superphylum Segmentata), there are serious reasons to place these phyla in different branches of the Animal Kingdom (Dodson, 1960; Hyman, 1940). Hyman has stated that "the exact steps in the evolution of the various grades of invertebrate structure are not and presumably never can be known. Statements about them are inferred from anatomical and embryological evidence and in no case should be regarded as established facts." This stricture applies with full force—perhaps with especial force—to the problem of the origin of the chordates. Nonetheless, there are good reasons for arranging the coelomate phyla (and some others) in two diverging series, each probably ultimately derived from some primitive, acoelous, flatworm (but not necessarily from any extant groups). One of the groups, comprising the protostome line, includes many phyla and culminates in the Annelida, Arthropoda, and Mollusca. They are united by a series of fundamental embryological characters. Cleavage is determinate and spiral. The mesoderm is derived from posteriorly placed stem cells, the multiplication of which produces a pair of ventral bands. The coelom is a *schizocoel*, formed by the splitting of these mesodermal bands. The blastopore of the embryo becomes the mouth of the adult, and it is from this trait that these phyla are called protostomes. Finally, trochophore larvae are widely distributed among the protostomes, and some zoologists believe that there must have been, in remote pre-Cambrian time, a trochophore phylum which was ancestral to all of the modern protostomous phyla. There are, of course, exceptions to all of these characters, especially among the Arthropoda. Yet the position of the Arthropoda in this series is quite clear, for their derivation from annelid ancestors is well established, as Raw (1953) himself has shown so clearly.

The other major branch of the Animal Kingdom comprises only five phyla: Chaetognatha, Pogonophora, Echinodermata, Hemichordata, and Chordata. These make up the deuterostome series, and they contrast with the protostomes in those fundamental embryological characters cited above. Thus cleavage is neither spiral nor determinate, development being regulative. Mesoderm is not formed from stem cells, but rather from outpocketings of the gut. This establishes the coelom simultaneously, and this is therefore *enterocoelous* rather than schizocoelous. The blastopore becomes the anus in these phyla, while the mouth is a new openlng, hence the term *deuterostome*. Development does not lead to any uniform larval type, but the Dipleurula larva is a sort of common denominator of echinoderm and hemichordate larvae. It establishes beyond a reasonable doubt that the radiality of adult echinoderms is secondary to the bilaterality of a remote Precambrian ancestor. If the Dipleurula larva gives any insight into the characteristics of that remote protechinoderm, it may also give some indication of the characteristics of the even more remote common ancestor of the deuterostome phyla, including the Chordata.

Raw emphasizes that apparent biological inconsistencies in his theory are unimportant because of the great antiquity of the events conjectured: the great reaches of geological time provide adequate opportunity for loss or obfuscation of important evidence. He does not extend the same charity to competing theories. Thus, while he apparently depends upon this principle to neutralize the complete lack of evidence of either morphological or biochemical homology of arthropodan and vertebrate skeletons, he feels that the crystalline character of the echinoderm skeleton disquali-

fies echinoderms as relatives of the chordates. Actually there is no reason to look for homologies between the chordates and adult echinoderms. The echinoderm theory of the origin of the chordates is based primarily upon embryological evidence, (with some biochemical corroboration) namely, mutual concurrence in the general deuterostome characters and especially the close correspondence of the Tornaria larva of the hemichordate *Balanoglossus* with the Bipinnaria larva of a starfish. Indeed, it was originally described as a larval starfish by Müller (1850). The correspondence is not merely superficial, but it extends to fine details. For example, the pattern of ciliary bands of the Tornaria larva is closely similar to that of some echinoderm larvae. The digestive system is similar in development, size and shape, and details of its tripartite subdivision into foregut, midgut, and hindgut. The coelom, too, arises in the same way, forms a similar series of three pairs of coelomic vesicles, and, to a limited extend, gives rise to similar derivatives. The degree of similarity is too great for explanation on any basis other than relationship. Thus, the remote ancestors of the chordates and echinoderms should have diverged long before the latter developed those traits which caused Hyman (1955) to "salute the echinoderms as a noble group especially designed to puzzle the zoologist." This Dipleurula theory was original with Bather (1900).

The relationship of echinoderms and hemichordates can, then, be stated with reasonable assurance. Since Bateson united the hemichordates with the chordates in 1885, the former have generally been recognized as a subphylum of the latter. Numerous zoologists, however, have considered the hemichordates to be an independent phylum, and Hyman (1959) has taken that position emphatically in her review. The presumed affinity of the hemichordates and chordates rests upon three characters: the notochord, the dorsal nerve tube, and the pharynx perforated by gill slits. The notochord of the hemichordates occurs only in the proboscis. It has also been homologized with the hypophysis, and hence its status as a notochord is very doubtful. The dorsal nerve tube, like that of chordates, arises by the inrolling of a medullary plate and, indeed, it is not completely separated from the ectoderm in some species. But it is confined to the collar, while the main nervous system of the body as a whole is an invertebrate type, solid, ventral cord. Hence this character, too, is equivocal. Gill slits in hemichordates may be very numerous, and they are closely similar to those of *Amphioxus* both in development and in details of morphology. Hyman (1959) feels that the correspondence of the gill slits and their skeletal supports is too detailed and precise to be accounted for except by relationship. As the other supposed homologies, however, are doubtful, except for the general agreement in the basic deuterostome characters, no direct descent can legitimately be postulated.

### THE DIPLEURULA THEORY REASSERTED

In summary, then, the Dipleurula theory of Bather is here reasserted. In remote pre-Cambrian time, the Dipleurula stock gave rise to divergent stocks. One line produced the aberrant echinoderms; the other produced the more typical hemichordates and the very progressive chordates. When Raw asks how the gill slits could have been formed *de novo*, the answer is much the one which he gave regarding the origin of the notochord: the embryological evidence may be taken at face value in the absence of any contrary evidence. The original mutation for the production of perforations at the anterior end of the digestive tract was a random event: it was preserved by natural selection because the organism was already feeding on minute particles, (like echinoderm larvae today) and the gill slits made this more efficient by permitting sieving of the food from the water. This development then gave selective value to any mutations tending to improve the gill system, such as the development of skeletal support. Respiratory function of the gills could not be very important for a small unaggressive animal with a large external surface relative to body volume, and it is probable that the respiratory epithelium was added to the gills only much later, again as a random mutation favored by selection because of increasing size of the organisms, more active predatory mode of life, and other factors. In the great reaches of time which Raw emphasizes, it is quite plausible that demonstrated

Darwinian processes could have resulted in the formation of the Chordata from a Dipleurula ancestor; that some of the less progressive chordates might have formed the Urochordata (tunicates) and the Cephalochordata (*Amphioxus* and its allies) with some degeneration in their modern representatives; and that the more progressive chordates then produced the ostracoderms and through them the great array of vertebrates which now dominate the world.

While this seems to me to be the most reasonable theory of the origin of the vertebrates in the present state of knowledge, it is nonetheless fully subject to the stricture of Hyman, quoted above. W. R. Brooks has said that "Suspended judgment is the greatest triumph of intellectual discipline." Until far more conclusive data are available than any now at hand, the problem of the origin of the chordates is one which calls for such a triumph.

### ADDENDUM ON LAMARCK

Bates (1960) has said that he does not like to see the name of Lamarck used as a dirty word, and the present writer agrees. Lamarck's contributions to zoology were of great and lasting value. He was second only to Linnaeus in his services to taxonomy. It was he who first saw the utility of contrasting vertebrates and invertebrates. Among the latter, where Linnaeus had felt the need for only two classes, Insecta and Vermes, Lamarck recognized twelve: Mollusca, Cirripedia, Annelida, Crustacea, Arachnida, Insecta, Vermes, Radiata, Polypes, Infusoria, Tunicata, and Conchifera. Some of these he described in very much the modern sense, while others, quite understandably, he treated less successfully. Needless to say, such great advances were based upon extensive studies of the animals and upon profound insight. Collectively, his work upon the invertebrates established the necessary foundation for the great progress in zoology which characterized the nineteenth century and in which Darwin participated so brilliantly. Another aspect of Lamarck's work is less well known, but equally noteworthy. In 1809, he wrote, "No body can possess life if its containing parts are not a cellular tissue, or formed by cellular tissue . . . Cellular tissue is the general matrix of all organization . . . Since the year 1796 I have . . . set forth these principles in the first lessons of my course." Thus he anticipated the cell theory of Schleiden and Schwann by more than 40 years. For these achievements he deserves a place of lasting respect among the most distinguished zoologists. Yet he has had the misfortune of having his name memorialized by his principal mistakes, inheritance of acquired characters and evolution by means of direct environmental induction of adaptations, together with inheritance of these acquired characters. The neo-Lamarckians do Lamarck a great disservice, for, by focusing attention on the major errors of this great zoologist (and many reputable zoologists have erred as badly without achieving so much), they detract attention from his just claims to fame among zoologists.

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# OXYGEN ISOTOPE PALEOTEMPERATURE MEASUREMENTS ON CRETACEOUS BELEMNOIDEA FROM EUROPE, INDIA AND JAPAN

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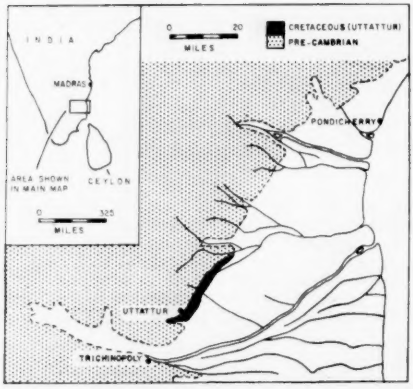
ABSTRACT—A number of Cretaceous Belemnoidea from northwest Europe, India, and Japan were analyzed and their paleotemperature record compiled from mass-spectrometric measurements. Their delta values in parts per mil are averages of whole rostra and, hence, represent average temperatures for the periods during which these were formed. They are related to the standard PDB-1. Of the assembly, some were analyzed to show variations in delta values during rostral growth, i.e., data was derived from examination of successive increments of powdered carbonate from the rostra. These are interpreted as seasonal variations of temperature by the author and are also related to PDB-1. The information so obtained is compared with that given by other fields of investigation. It is demonstrated that from initially coolish conditions in Neocomian times, two Cretaceous climatic maxima occurred—in the Albian and later in the Coniacian-Santonian (Lower Senonian). The effects of these extended from Europe into India, but are not apparent in the single Japanese specimen analyzed. Subsequently, climatic deterioration took place followed by stable, lower temperature conditions in the Maestrichtian. It is possible that the Cretaceous poles lay near the present day Bering Sea and South Africa respectively with the equatorial region running from the southern United States through Europe. The Jurassic equator probably occupied a closely similar position and the principal climatic distinction between the two periods is the greater equability of the earlier.

## INTRODUCTION

THE method of determining ancient temperatures by assaying the relative amounts of $O^{18}$ and $O^{16}$ in organic carbonates was originally devised by Urey (1947, 1948). Measurements by means of sensitive mass-spectrometers have been used by a number of workers as indicative of past climates. Epstein, Buchsbaum, Lowenstam & Urey (1953) have noted in detail the chemical techniques by means of which carbon dioxide gas may be obtained from carbonate samples. This paper deals with data obtained by such analyses of Cretaceous Belemnoidea from Northwest Europe, India and Japan. Since recrystallized carbonates do not retain the paleotemperature record satisfactorily, altered (i.e., opaque) Belemnoidea were not utilized. The rostra are the most commonly preserved parts of Belemnoidea and they consist of stable, megascopic crystals of calcite radially arranged around the apical line. While normally translucent, these become opaque if any change in preservation takes place. In order to ensure complete removal of any organic material that may be present, carbonate samples extracted from the Belemnoids with a dental drill and powdered in a mortar were subsequently roasted following the techniques mentioned above. Later reaction with 100% phosphoric acid produced carbon dioxide. The standard gas used by Urey *et al.* (1951) was $CO_2$ obtained from a *Belemnitella americana* from the Peedee formation (Upper Cretaceous: Maestrichtian) of North Carolina, U.S.A. This standard is usually known as PDB-1 and by definition it has no delta (i.e., its delta can be regarded as being zero). This standard was not available for the present work and so a new one was used. The new standard was made from a number of Jurassic Belemnoidea from the island of Skye off the coast of Scotland; measurements of it against NBS-Solenhofen Limestone reference sample number 20 (which, according to Craig, 1957, gave an $O^{18}$ delta value of $4.14‰$ against PDB-1) showed that it has a delta value very close to zero. In the analyses carried out, several Skye standards were used and the necessary corrections were applied to the machine results so that the whole series is related to PDB-1. The question of the isotopic composition of the oceans in Cretaceous times is important in calculation of the actual temperatures.




TEXT-FIG. *1*—Map showing locality of specimens of *Belemnites fibula* obtained from the Uttattur stage (Upper Albian section) of the Cretaceous of the Trichinopoly district.

Urey *et al.* (1951) assumed that the mean ocean delta was the same then as now. Epstein & Mayeda (1953) estimated the latter to be $0.00‰$ with an average deviation of $\pm 0.1$. From this, it is apparent that PDB-1 is practically equivalent to $CO_2$ equilibrated with average ocean water at 25°C. Temperature was related to $\delta$ by the following equation (Epstein *et al.*, 1953):

$$t = 16.5 - 4.3\ (\delta - A) + 0.14\ (\delta - A)^2$$

where A is the delta value of the water in which the calcium carbonate is precipitated, an unknown in paleooceans. The author has used this as a conversion formula taking A as zero (i.e., assuming the mean Cretaceous ocean delta to be the same as that of present day seas). The comparative values of paleotemperature measurements are unaffected by this procedure (which was also adopted by Dorman & Gill 1959 among others). The Lowenstam & Epstein (1954) "reasonable" temperature range of 0–30°C. is accepted as satisfactory for the majority of measurement, although it is to be expected that some may fall above it. Mean rostral temperatures were derived by cutting a complete cross-section representing accumulative growth, cleaning it of all contaminants and grinding it to a powder, the necessary aliquot for investigation being taken from this. A number of analyses was carried out to determine the variation of temperature with growth (v. Bowen, 1961a,b) and hence the temperature range through which the animal lived. The method utilized was to grind off successive increments of powdered carbonate from the rostra, being careful to maintain the grinding parallel to the growth layers. Mass-spectrometric determinations were made on close to three dozen specimens of Belemnoidea.

## DETAILS OF SPECIMENS EXAMINED

A. *Northwest Europe:*

(1) *England.*—Three specimens were collected from the Gault clays of Folkestone, Kent, and are of Albian age; another five came from the top of the same stage (aequilateralis-dispar zones) at Cambridge (Cambridge Greensand). One specimen originated in the Speeton Clay (Valanginian-Hauterivian) of Speeton, 4 miles South-East of Filey, Yorkshire. A tenth specimen was collected from the Belemnite marls of Chilcombe 2 miles East of Winchester, Hampshire and is either Upper Cenomanian or Lower Turonian in age.

(2) *Belgium.*—Five specimens of *Belemnitella mucronata* were collected from the Maestrichtian of two localities—Ciply near Mons in Hainaut and the province of Brabant. From St. Vaast about 10 miles east of Mons, another Cretaceous specimen was obtained. Finally, three additional Belemnoids were collected in Hainaut (Craie de Trireieres) and are assigned to the species *B. quadrata.*

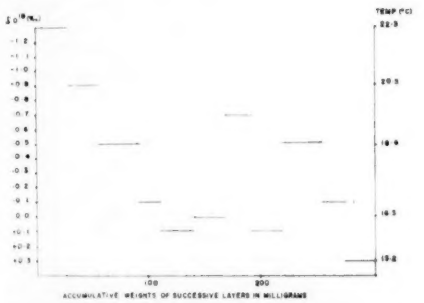
(3) *France.*—Four specimens were collected from the Aptian. Two from the upper part of this stage, namely the Gargasian (of which the characteristic Ammonoid is *Oppelia nisus*), are of the species *Neohibolites semicanaliculatus.* A third (of *B. neominimus*) came from Wissant near Calais and a last one from the same stage at Bevoule. Three Albian specimens were analyzed—all came from the cliffs of Blanc Nez in the Pas de Calais. A *Belemnitella mucronata* from the Campanian of Meudon (Seine) and an *Actinocamax rerus* from the Coniacian-Santonian complete the list. The paleogeography of North-West Europe in the Cretaceous has been extensively studied. It is interesting to note that a gulf arising from the north occupied the Yorkshire area of

England in Valanginian-Hauterivian times and in this flourished a northern fauna including the large Belemnoid *Cylindroteuthis;* no inter-communication between this and the Mediterranean area existed until Aptian times. Then such southerly Ammonoids as *Hoplites deshayesi* are found associated with the Belemnoids. By the Upper Cretaceous, the Paris Basin was in broad contact with the Alpine Sea and the Chalk seas spread through northern Europe into South Russia and the Middle East.

B. *India:* Specimens of *Belemnites fibula* were examined from the Uttattur stage of the Cretaceous of the Trichinopoly district. Here, the Cretaceous lies to the east of the PreCambrian shield area of gneisses and charnockites. The Uttattur beds themselves comprise silts, shales and clays with ferruginous, phosphatic and calcareous nodules. They are abundantly fossiliferous with such corals as *Thecosmilia geminata*, many ammonoids, e.g. *Acanthoceras mantelli, Lytoceras timotheanus, Baculites vagina,* pelecypods like *Gryphaea columba* and gastropods, e.g. *Turritella nodosa.* Besides *B. fibula,* they also contain *Belemnites stilus.* Three divisions exist in the stage, the lower two being of Upper Albian and Cenomanian age and the Upper Uttattur being Lower Turonian in age. The Belemnoidea occur in the basal limestones and clays and are therefore of Upper Albian age.

At this time, the Indian shield was flanked to the north by the Himalayan geosyncline, which communicated to the east with the Sumatra-Java geosyncline (and thus indirectly with the Westralian geoysncline of Western Australia). To the northwest lay the easternmost limits of the European Chalk Sea to be; to the southwest lay the Mozambique channel.

C. *Japan:* A single specimen of *Neohibolites miyakoensis* was obtained from the Albian for analysis. This was collected 3 meters below the top of the Tonohata conglomerate and the locality was Hiraiga, Tanohata-mura, Shimohei-gun, Iwate prefecture. This is in the northeastern part of the main island of Honshu. During Albian times, most of the Japanese islands were land—part of the great Cathaysian shield. However, the eastern part of Honshu was marine, forming a part of the Kuril geosyncline which extended south (through the Mariannas arc) to join the Papuan geosyncline and the Westralian geosyncline.




TEXT-FIG. 2—Data derived from a seasonal variation analysis carried out on the belemnoid obtained from the Speeton clay (Valanginian-Hauterivian) of Speeton, Yorkshire, England. The range of temperature during ontogeny was 7.1°C. and there are three maxima alternating with three minima—thus, the animal probably lived for a minimum of three years.

## PALEOTEMPERATURE RESULTS

Data derived from analyses of whole specimens

A. *Northwest Europe:*

(1) *England.*

Locality and horizon: Folkestone, Gault Clays (Albian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperatures in °C. |
|---|---|---|
| 1 | −0.80 | 20.0 |
| 2 | −1.02 | 21.0 |
| 3 | −1.50 | 23.3 |

Locality and horizon: Cambridge, Cambridge Greensand (Upper Albian: aequilateralis-dispar zones)

| Specimen Number | Ave. corr. delta in parts per mil | Temperatures in °C. |
|---|---|---|
| 1 | −1.00 | 20.9 |
| 2 | −1.05 | 21.2 |
| 3 | −1.05 | 21.2 |
| 4 | −1.20 | 21.9 |
| 5 | −1.40 | 22.8 |

Locality and horizon: Speeton, Speeton Clay (Valanginian-Hauterivian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | 0.0 | 16.5 |

TEXT-FIG. 3—Data derived from a seasonal variation analysis carried out on the belemnoid collected from the Belemnite Marls at Chilcombe, England—these are of Upper Cenomanian or Lower Turonian age. The range of temperature through which the animal lived was 12.6°C. and again there were three climatic maxima alternating with three minima.

Locality and horizon: Chilcombe, Belemnite Marls (Upper Cenomanian or Lower Turonian)

| Specimen | Ave. corr. delta | Temperature in °C. |
|---|---|---|
| 1 | +0.70 | 13.5 |

2. *Belgium:*

Locality and horizon: Ciply (Maestrichtian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.43 | 18.4 |
| 2 | −0.46 | 18.5 |
| 3 | −0.78 | 20.0 |

Locality and horizon: Brabant (Maestrichtian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.78 | 20.0 |
| 2 | −0.84 | 20.2 |

Locality and horizon: St Vaast (Cretaceous)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.27 | 17.7 |

Locality and horizon: Hainaut (Craie de Trireieres)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.33 | 17.9 |
| 2 | −0.85 | 20.2 |
| 3 | −0.98 | 20.8 |

3. *France:*

Locality and horizon: Clansayes (Gargasian—Upper Aptian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −1.02 | 21.0 |

Locality and horizon: Vancl. (Gargasian—Upper Aptian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in C. |
|---|---|---|
| 1 | −0.89 | 20.5 |

Locality and horizon: Wissant (Aptian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −1.59 | 23.7 |

Locality and horizon: Bevoule (Aptian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.62 | 19.2 |

Locality and horizon: Blanc Nez (Pas de Calais—Albian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −1.39 | 22.7 |
| 2 | −1.81 | 24.7 |
| 3 | −1.89 | 25.1 |

Locality and horizon: Meudon (Seine—Campanian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.87 | 20.3 |

Locality and horizon: France (Coniacian—Santonian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 8 | −1.20 | 21.9 |

B. *India:*

Locality and horizon: Karai, Trichinopoly (Upper Albian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −1.10 | 21.4 |
| 2 | −1.25 | 22.1 |
| 3 | −1.31 | 22.4 |

C. *Japan:*

Locality and horizon: Hiraiga, Honshu (Albian)

| Specimen Number | Ave. corr. delta in parts per mil | Temperature in °C. |
|---|---|---|
| 1 | −0.06 | 16.8 |

A number of analyses were carried out with the object of showing the variation of temperature with growth during those portions of the ontogenies of the Belemnoidea selected in which rostral growth actually occurred. Some of the data are shown on the accompanying figures and their interpretation by the author is based upon the assumption that they record seasonal temperature variations. Other explanations are of course available, e.g. they may denote migrations from cooler to warmer bodies of water or vice versa. However, Lowenstam & Epstein (1954) have shown that in some cases the belemnoid temperature trends parallel those of associated benthonic forms—here, the relevant belemnoids (though nektonic in habit) must have passed much of their lives in the seasonal climatic ranges of their areas of burial. Thus, while there is no actual evidence of migration, some evidence against it exists. This latter is of course confirmatory of seasonal variation. The same objection may be brought against the acceptance of a suggestion of P. L. Cloke that the incremental analyses represent not temperature, but salinity variations. Until some evidence is available to the contrary, the author believes the hypothesis adopted herein to be the only justifiable one. The analyses made show a range of variation of 2° to 8°C. Sometimes, a range as great as 12°C. within the life cycle of a single belemnoid occurred, however. Most of these animals probably lived through 3 or 4 years at the most and some of them through a lesser span—assuming the highs represent summers and the lows winters in the seasonal variation records. Within particular assemblages from a specific horizon, these and other investigations show that the temperature fluctuations are small enough to indicate relatively uniform climatic conditions over the time interval in which the zonal sedimentary deposits accumulated.

## CRETACEOUS PALEOCLIMATOLOGY

According to C. E. P. Brooks (1949), in the region between 40 and 90°N. lat. the Cretaceous was a rather cool period of time. His figures, based upon such factors as continentality, ocean currents and vulcanicity—all of which are more or less speculative—are divided into "observed" and "calculated" results. For the Middle Cretaceous, they are 5°C. (41°F.) and 6.6°C. (44°F.) respectively. For the Upper Cretaceous, he gave the figures 5°C. and 3.8°C. (39°F.). Brooks stated "these figures have no pretensions to any great degree of accuracy," a point well illustrated by comparison with an estimate given by Dorf (1955). He gave 20°C. (68°F.) as the approximate mean annual temperature for the Upper Cretaceous of the zone between latitudes 40° and 50°N. in the western United States. This is at least four times greater than the Brooks figures. Perhaps the best evidence—other than $O^{18}$ measurements—of the distribution of climatic belts in the Cretaceous is derived from study of three groups of animals, namely rudistid corals, orbitolinid foraminifera and dinosaurs. Of the first, Brooks noted that their distribution "is the strongest point in favor of the displacement of the poles . . . (it) requires a much greater northward displacement of the thermal equator than at present." As the Termiers (1960) illustrate, the rudistids are found in the Gulf Coast area of North America, scattered through Southern Europe and North Africa plus the Middle East and even occasionally getting as far north as Germany and as far south as Somaliland and into the regions of the Sumatran and Papuan geosynclines. Orbitolines are roughly coincident in their distribution. The dinosaurs are somewhat more widely distributed—thus in the Neocomian, they are found in South America, South Africa and Madagascar, India and Eastern Australia as well as in North America, Europe, North Africa and East Asia. All this data is valuable both in indicating a different distribution of climatic zones from that now existing and also in aiding the determination both of the positions of the Cretaceous climatic zones and, also of the Cretaceous poles. Another field of investigation which has proved fruitful in a number of ways (though its utility in the Cretaceous is not very great) is that of paleomagnetic measurement. In this, it is assumed that over a period of time exceeding a few thousand years the magnetic field of the earth approximates to a geocentric axial dipole and has always done so. The origin of this field is not certain although most workers think that the fluid core of the planet acts

as a self-exciting dynamo (Elsasser, 1956). If the average geocentric dipole is invariably directed along the axis of rotation, then pole positions calculated from analyses of rock group magnetism approximate closely to or coincide with those of the geographic poles. Suggested positions of the poles for various geological periods based upon paleomagnetic measurements were joined together to form a pole-wandering curve as early as 1954 (Creer *et al.*). Later more detailed curves were constructed. Cox & Doell (1960) discussed Cretaceous virtual geomagnetic poles and gave a figure plotting their positions. One obtained by measurements on the Wealden sediments of the Isle of Wight, England lies almost mid-way between the present pole and Victoria Island off the North-West Territories of Canada. Measurements were made on the Dakota sandstone (Colorado Plateau, U. S.) and yielded a pole roughly mid-way between the present pole and the East Siberian Sea. Madagascan measurements on Turonian lavas and dykes gave the polar position as in northwestern Alaska while other analyses of the Inkstone red shales (Lower or Middle Cretaceous) of Japan resulted in a pole in the northeastern Pacific. These are the only data so far available that have been obtained from strata known certainly to be of Cretaceous age.

## INTERPRETATION OF PALEOTEMPERATURES

At the present time the variation of temperature with latitude attains a maximum of about 60°C. The annual average reaches a maximum of 30°C. in the equatorial region and a minimum of −20°C. in the polar one. A variation of ±10°C. may be expected. This is of course most marked between summer and winter in the polar areas and becomes less and less significant until there is negligible fluctuation on the equator. It is interesting to compare these figures with those derived from the analyses recorded here. The minimum temperature recorded from a whole specimen is 13.5°C. (Chilcombe, Hampshire, England: Upper Cenomanian or Lower Turonian) and the maximum is 25.1°C. (Blanc Nez, Pas de Calais, France: Albian) giving a range of 11.6°C. Since the temperature tolerance of the Belemnoidea which were nektonic in habit is not known, the inferences which may be drawn from this information are fewer than might be desired. Nevertheless, it is obvious that these animals could colonize rather cool bodies of water and also spread into warm ones. It is most unlikely that polar ice existed for more than a small part of the Cretaceous and although the records of seasonal variation clearly establish the existence of seasons, it is apparent that the Cretaceous was a period of less climatic extremes than those now existing. Previous work carried out on Jurassic Belemnoidea from all parts of the world and also on other Cretaceous material from central Europe and Australia (Bowen, 1961) show that there was an appreciable cooling-off from Jurassic to Cretaceous times. The results recorded in the present paper may now be considered stratigraphically.

*Lower Cretaceous*

Valanginian-Hauterivian: Speeton Clay, Speeton, England—16.5°C.
Aptian: Wissant, France—23.7°C. Bevoule, France—19.2°C.
Upper Aptian: Clansayes, France—21.0°C. Vancl., France—20.5°C.
Albian: Gault Clay, Folkestone, England—20°C., 21.0°C. and 23.3°C. Blanc Nez, Pas de Calais, France—22.7°C., 24.7°C., 25.1°C. Hiraiga, Honshu, Japan—16.8°C.
Upper Albian: aequilateralis-dispar zones, Cambridge Greensand, Cambridge, England—20.9°C., 21.2°C., 21.2°C., 21.9°C., 22.8°C., Uttattur stage, Karai, Trichinoploy, India—21.4°C., 22.1°C., 22.4°C.

*Upper Cretaceous*

Upper Cenomanian or Lower Turonian: Belemnite Marls, Chilcombe, Hampshire, England—13.5°C.
Coniacian-Santonian: France—21.9°C.
Campanian: Meudon, Seine, France—20.3°C.
Maestrichtian: Ciply, Brabant, Belgium: 18.4°C., 18.5°C., 20.0°C. Brabant, Belgium—20.0°C., 20.2°C.

Working with material from England, Urey *et al.* (1951) suggested that there took place a progressive increase in temperature from Albian times until the Coniacian-Santonian and this was followed by a fall and levelling off in the Maestrichtian.

That this view required modification became evident from analyses made by Lowenstam & Epstein (1954) and Bowen (1961a). It is apparent that there were much lower temperatures in the Cenomanian and Turonian than was the case in the Albian. In

the Danish Cenomanian, the first pair of authors recorded temperatures as low as 15.4°C. and the latter cited 16.8°C. from the same stage in Poland. In the present work, a Belemnoid either of Cenomanian or Lower Turonian age gave a reading of 13.4°C. Thus a climatic minimum took place during this period of time and this is true all over Europe—the last specimen mentioned came from England. Earlier there was a maximum in the Albian—e.g., Lowenstam & Epstein (1954) gave figures varying between 21.8°C. and 24.5°C. for specimens of *Neohibolites minimus* derived from the French Albian; in the present paper, the average temperature of three specimens from the Gault of Folkestone was 21.5°C., of five from the aequilateralis-dispar zones of the Cambridge Greensand was 21.6°C.. of three from the Pas de Calais was 24.2°C., and of three from the Upper Albian of Karai, India, was 21.9°C.

The situation in the Far East is rather significantly different, however. From Japan, a reading of 16.8°C. was obtained and both Lowenstam & Epstein (1954) and Dorman & Gill (1959) gave low-temperature readings on Albian and Aptian material respectively. Work by the present author on material of from Albian to Turonian age gave an average reading of 19.3°C. It was obtained from Western Australia (v. Bowen, 1961b).

This leads to the view that the Albian climatic maximum extended over Europe and India, but not to the Far East. Another climatic maximum occurred in Coniacian-Santonian (=Emscherian, i.e., Lower Senonian) times when temperatures of 21.9°C. (present paper), 21.5°C. (Bowen, 1961a), 23.2°C. (Lowenstam & Epstein, 1954), etc. were recorded. The second figure is from Poland and the third from England. Subsequently, a gradual decline into the Maestrichtian occurred and has been discussed in detail by the author (Bowen, 1961). It is apparent that in the Cretaceous the climate was more diversified than in the Jurassic. It is also clear that the evidence from corals and other animals adduced earlier is confirmed and that the Cretaceous equator certainly ran through Europe. American data indicates its westerly continuance through the southern United States.

India presents a very interesting problem. From Jurassic specimens, the author has obtained temperature readings of 18.5°C. (Kimeridgian)—substantially lower than the Cretaceous reading. The interpretation of this may be that India underwent a migratory movement from a position south of the Tethys to a position north of it during the late Mesozoic. At the present, the author is analyzing specimens of Belemnoidea obtained from South Africa—actually from the northern bank of the Usutu river, Manyola Drift, Mozambique, and from the Aptian. Preliminary results may throw some light on the pole position in the Cretaceous. They show unusually low temperatures—at a time when in Europe a climatic maximum was approaching. It appears possible that the poles were located somewhere in the regions now occupied by the Bering Sea in the north and South Africa in the south. The equator which is known to have been situated in the southern United States and European position alluded to previously is consistent with this interpretation. There is some evidence that the pole positions and that of the equator were much the same throughout the Mesozoic and thus the low-temperature readings obtained by analyses of specimens from the Callovian of Alaska are highly relevant to this interpretation. Work is being continued with a view to adducing additional evidence in the matter. That it is essential to any consideration of pole-equatorial relationships in the Mesozoic is apparent from the statement of Cox & Doell (1960) that

> "paleomagnetic measurements for the Mesozoic and early Tertiary present an interesting problem; although the preceding Permian and following post-Eocene results are each internally consistent, the geomagnetic pole positions from the Mesozoic and early Tertiary are quite scattered. Some impressively consistent results have been obtained for individual Triassic formations and the distribution of results from North America and Europe to some extent suggests relative drift. However, the scatter between mean formation directions is quite large and weakens the conclusion that a relative displacement has taken place. The paleomagnetic results from the Jurassic are at least as scattered as those for the Triassic and no conclusive statements regarding drift or wandering can be made."

Of the Cretaceous, they wrote that "the paucity of paleomagnetic information has

already been discussed . . . thus . . . the North American (and possibly European) field configurations for Cretaceous . . . time are far from certain and without such a well-defined reference position, the drift interpretations . . . may be questioned."

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1085–1087, 1 TEXT-FIG., SEPTEMBER, 1961

# THE FIRST AMERICAN RECORD OF *LANTANOTHERIUM* FILHOL*

S. DAVID WEBB

ABSTRACT—Part of a lower jaw from the Bopesta formation, Barstovian, of California is the first American record of *Lantanotherium* Filhol (1888).

## INTRODUCTION

IN 1949 Robert L. Shultz and Richard H. Tedford collected vertebrate fossils for Chester Stock from the Bopesta formation in Southern California (Buwalda, 1934). One of their important discoveries was the lower jaw fragment of *Lantanotherium* Filhol (1888). This erinaceid insectivoran has been recorded previously from European sites of Vindobonian age and questionably from China (Viret, 1940, p. 53).

The locality and specimen numbers refer to the American Museum of Natural History (AMNH), the California Institute of Technology (CIT), and the Los Angeles County Museum (LACM).

## ACKNOWLEDGMENTS

I wish to thank Theodore Downs of the Los Angeles County Museum for loaning the specimen here described to the University of California Museum of Paleontology, and E. H. Colbert and Rachel Nichols of the American Museum of Natural History for making specimens and facilities in their charge available to me. I am grateful to R. A. Stirton, Donald E. Savage, and Gideon T. James for their criticism of the manuscript, and particularly to Malcolm C. McKenna whose advice and encouragement have been instrumental in preparing this paper. The illustrations are by Howard Hamman.

## INSECTIVORA
### ERINACEIDAE
### ECHINOSORICINAE
### LANTANOTHERIUM *sp.*

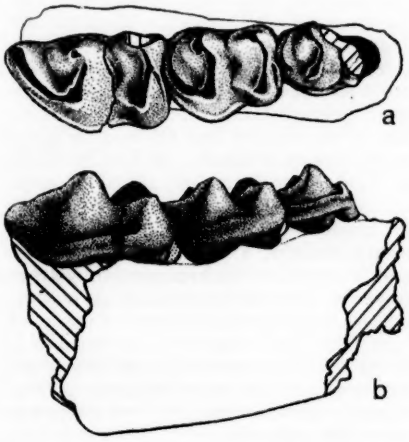
Text-fig. 1

*Material.* LACM (CIT) no. 5284, portion of left mandible with three molars in place, most of $M_3$ talonid broken off. Collected by Richard H. Tedford.

*Horizon and Locality.* Bopesta formation, Barstovian, northeast Cache Peak area, northeast of Monolith, Kern County, California, CIT locality 502 (V 508), Tehachapi Quadrangle, Corps of Engineers Map, 1942, scale 1:62,500′, progressive grid coordinates 1273.6, 1358.2.

*Description and Diagnosis.* The bulbous appearance of the molars recalls the exodaenodonty of dimylids (Hurzeler, 1944, p. 7). This swelling of the sides of the crown over the base is greater on the labial side of each tooth. The posterolingual divergence of the molar row from the midline of the horizontal ramus, typical of erinaceids and most other placental groups, is emphasized in this form by the fact that the molars become less exodaenodont posteriorly.

$M_1$ is 3.5 mm. long. The trigonid is twice




TEXT-FIG. 1—*Lantanotherium sp.*, left lower jaw, ×7.5. a, occlusal view; b, labial view.

* A contribution from the University of California, Museum of Paleontology.

the length of the talonid and slightly broader. The conical metaconid is directly lingual to the subtriangular protoconid. The protolophid is a narrow transverse crest, depressed in the middle. The anterior trigonid cusp, here termed the paraconid, is much lower than the protoconid and metaconid (for a discussion of other possible homologies of this cusp see Butler, 1948, p. 462). It is widely separated from the metaconid. The anterolingually-oriented paralophid must have been as effective a shearing crest as in *Amphechinus* Aymard (1849) or *Metechinus* Matthew (1929). The narrow trigonid valley slopes linguad, opening broadly at the crown base between the paraconid and the metaconid.

The entoconid and hypoconid of $M_1$ occupy extreme positions the same distance behind the metaconid and protoconid respectively. The lingual part of the entoconid is missing from this specimen. From the posterior wall of the entoconid a continuous occlusal surface slopes back across the paralophid of $M_2$ into its trigonid valley, The hypoconid of $M_1$ is triangular. A longitudinal ridge on each side connects the entoconid and the hypoconid to the posterior face of the trigonid. Although these ridges are low anteriorly, they do not fade out before contacting the trigonid base as they do in *Erinaceus* and advanced species of *Amphechinus*. The Asian species of "*Amphechinus*" (i.e. *Palaeoscaptor* Matthew and Granger (1924)) have these same ridges, except that on some specimens, AMNH no. 21670 for example, the ridge from the hypoconid (crista obliqua) contacts the posterior face of the trigonid near the midline of the tooth instead of labially. In LACM (CIT) no. 5284 a distinct cuspule is visible on the anterior third of the longitudinal ridge from the hypoconid. The hypolophid is broad and nearly straight; a faint widening near its middle represents the hypoconulid. A strong posterior cingulum connects the hypoconulid with the posterolabial corner of the crown base. The labial cingulum is as broad as in *Erinaceus;* it is concealed at the base of the hypoconid by the exodaenodonty of that cusp. It narrows anteriorly and disappears below the paraconid.

$M_2$ is 2.4 mm. long. The trigonid is shorter than in $M_1$ and the metaconid and protoconid are farther apart and connected by a stronger crest. A paraconid is not clearly distinguishable. The paralophid is recurved lingually, restricting the outlet of the trigonid valley. The openness of the trigonid, however, as measured by the angle between the paralophid and the protolophid, is as large in this genus as in *Palaeoscaptor* (about 45°).

The talonid of $M_2$ is narrower relative to the width of the trigonid than on $M_1$. The entoconid is conical on the lingual side, flat and nearly vertical on the face rising from the talonid basin. The posterior cingulum does not extend to the posterolabial base of the tooth as in $M_1$.

The trigonid of $M_3$ is 1.1 mm. long, whereas that of $M_2$ is 1.4 mm. Other differences in appearance are related to greater wear on $M_2$. Only the anterior half of the posterior root and a small anterolabial portion of the crown bearing a cuspule 0.6 mm. behind the protoconid remain of the talonid of $M_3$. This cuspule is the serial homologue of the one, described on $M_1$ and found in a similar position on $M_2$, that appears on the anteroposterior ridge from the hypoconid. The posterior rim of the alveolus is 1.0 mm. posterior to the trigonid. The position of the cuspule and the alveolus suggest that the talonid had a length of about 1.0 mm.

The mandible has a depth of 3.7 mm. on the lingual side below $M_1$. The greatest width, just anterior to $M_1$, is 2.0 mm. The sides of the mandible are nearly flat. There is no direct evidence of a large incisor root below the anterior end of $M_1$. The fracture through a point just in front of $M_1$, however, may be due to the presence of an incisor alveolus; if the alveolus were not present, this would seem to be the strongest part of the ramus. No foramina are visible.

### AFFINITIES

LACM (CIT) no. 5284 resembles both *Palaeoscaptor* Matthew and Granger (1924) and *Lantanotherium* Filhol (1888) in the greatly elongate paralophid of $M_1$, in the open trigonids of $M_2$ and $M_3$, and in the connection of the hypoconid and the entoconid to the trigonid each by a longitudinal ridge. *Palaeoscaptor* and *Lantanotherium*, however, are believed to be primitive members of different lines of erinaceid evolution.

They have been placed in different subfamilies principally on the basis of features of the upper dentition and skull. The relatively large size of $M_3$ and its well-developed talonid indicate that LACM (CIT) no. 5284 is an echinosoricine of the genus *Lantanotherium*. This specimen differs from *Galerix* and *Pseudogalerix* in having the metaconid placed directly lingual to the protoconid and in the lack of a clear paraconid on $M_2$ and $M_3$. In size and bulkiness this specimen particularly resembles *Lantanotherium robustum* Viret (1940).

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# NOMENCLATURAL NOTES

## CHANGE OF NAME FOR A CRETACEOUS CHIMAEROID

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Characteristic fossil chimaeroid egg-cases ranging in age from Jurassic to Oligocene were described as six new species and referred to a new form-genus *Chimaerotheca* by Brown (1946d). Among these, the name *C. wyomingana* was given (*ibid.*, p. 263) to a specimen from the Upper Cretaceous Mesaverde formation near Laramie, Wyoming. This specimen was previously named *?Elasmodus gilli* by Hay (1930a, p. 615) and now becomes *Chimaerotheca gilli* (Hay) Brown.

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## SUPPRESSION OF THE NAME *TASMANITES ROCKVILLENSIS*

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It has been brought to my attention by Mr. Richard Sheppard of the Johns Hopkins University that the specimen named *Tasmanites rockvillensis* is in reality an inorganic concretion. This species was described in the Proceedings of the Pennsylvania Academy of Science, v. 32. p. 186–187.

Accordingly, I would like to have this name suppressed with a promise to my paleobotanical colleagues that I will not invade their domain again.

JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1088–1096, 2 TEXT-FIGS., SEPTEMBER, 1961

# PALEONTOLOGICAL NOTES

## REVISED IDENTIFICATIONS OF SOME MISSISSIPPIAN CORALS DESCRIBED IN U.S.G.S. BULLETIN 1071-F[1]

WILLIAM J. SANDO
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Studies of Mississippian coral faunas from the western United States made by the writer after U.S.G.S. Bulletin 1071-F went to press necessitate changes in the identification of some of the corals described therein. The anomalous stratigraphic positions of certain taxa led the writer to question some of the previous assignments, and these suspicions were confirmed by careful re-examination of the material.

Specimens designated *Caninia* aff. *C. arcuata* Jeffords on p. 175 (USGS colln. 13905, 13917, 13920, and 15774) are now thought to belong to a dendroid species of *Diphyphyllum*, and are here designated *Diphyphyllum* sp. Species belonging to the *Caninia cornucopiae* group have an internal structure similar to the corallites of *Diphyphyllum*. The two taxa are easily differentiated in complete specimens because the *Caninia cornucopiae* species group includes only solitary forms whereas *Diphyphyllum* includes only colonial forms. Furthermore, species of the *Caninia cornucopiae* group in neanic stages have long major septa arranged similar to the septal plan of certain zaphrentoid genera, such as *Zaphrentites*; septa become amplexoid in the later cylindrical phase. In corallites of *Diphyphyllum*, septa are amplexoid throughout growth. Only under exceptional circumstances can can fragmentary corallites of *Diphyphyllum* be distinguished from fragments of the cylindrical phase of the *Caninia cornucopiae* species group. Re-examination of the Williston basin material revealed the following morphological features indicative of fragmented corallites of *Diphyphyllum:* 1) One of the specimens shows a small bud or offset arising by lateral increase, a mode of reproduction that is common in *Diphyphyllum* but unknown in the *Caninia cornucopiae* species group. 2) The corallum illustrated in plate 17, figure 7 is nearly complete, lacking only the tip, and exhibits amplexoid septa in the earliest stage present; if this specimen belonged to the *Caninia cornucopiae* species group, the neanic stage represented would have a zaphrentoid septal plan. 3) Many of the specimens are considerably longer and more vermiform than characteristic specimens of the *Caninia cornucopiae* group. The revised identification is supported by the known stratigraphic distribution of the forms in question. *Diphyphyllum*, commonly in the form of fragmented coralla, is common in the upper part of the Madison group and its equivalents in the western United States (Zone D of Sando and Dutro, 1960). The *Caninia cornucopiae* group may be restricted to the lower Lodgepole limestone in this area. The Williston basin specimens are all from the Charles formation and upper part of the Mission Canyon limestone, stratigraphic positions that coincide with the known distribution of *Diphyphyllum* and that would conflict with the known distribution of the *Caninia cornucopiae* species group in the Madison.

The two specimens in USGS colln. 15757 questionably referred to *Cleistopora placenta* (White) on p. 182 are now thought to represent a species of *Michelinia* and are here designated *Michelinia?* sp. Both specimens appear to represent immature coralla. Further investigation of one of these revealed the presence of tabulae, rather than reticular tissue in the interior of the corallites, which suggests *Michelinia* rather than *Cleistopora*. This revised identification is supported by the known stratigraphic distribution of the two genera. *Cleistopora* may be restricted to a narrow interval near the middle of the Lodgepole limestone (lower part of Zone $C_1$ of Sando and Dutro, 1960), whereas *Michelinia* ranges from middle Lodgepole into higher beds. The Williston basin specimens were collected from the

[1] Publication authorized by the Director, U. S. Geological Survey.

lowermost part of the Mission Canyon limestone.

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## WOLFCAMPIAN FUSULINID FROM INGLESIDE FORMATION, OWL CANYON, COLORADO

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A single but well preserved specimen of *Triticites ventricosus* (Meek and Hayden) was found near the base of the Ingleside formation at the type locality, Owl Canyon, Colorado. The specimen was about 17 feet above the highest arkose of the Fountain formation. The partial section is as follows (modified from Chronic, 1957):

Basal Ingleside formation:

| | |
|---|---|
| 5. Limestone, gray, resistant | 21′ |
| 4. Sandstone, pink, fine-grained, streaks of coarse white sandstone with broken crinoid stems, contains *Triticites ventricosus* (Meek and Hayden) about 6 feet above base. | 24′ |
| 3. Shale and sandstone, shale red, sandstone pink, one gray limestone in middle | 7′ |
| 2. Sandstone, red, fine to medium-grained | 4.5′ |

Fountain formation 566′:

| | |
|---|---|
| 1. Arkose, conglomerate, sandstone, shale and minor limestone, red, gray, pink and white | 566′ |

Precambrian.

The specimen was collected about 100 yards north of highway U. S. 287 where it passes through the Ingleside hogback at Owl Canyon (E ½ NW ¼ sec. 12, T. 9N., R. 70W.). An intensive search was made in the area but other fusulinids were not found.

The fusulinid identified as *Triticites ventricosus* (Meek and Hayden) has 5 volutions and is 5.3 mm. long and 2.4 mm wide. The outside diameter of the proloculus is 230 microns. Wall structure, chomata and fluting are typical of the species (text-fig. 1).

The Ingleside formation at Owl Canyon is 194 feet thick, and consists of interbedded pink and red fine-grained sandstone and gray limestone. It overlies the Fountain formation and is overlain by the Satanka shale. The occurrence of *Triticites ventricosus* (Meek and Hayden) in the basal beds of the Ingleside indicates a Wolfcampian age for the Ingleside at the type locality although the position of the Wolfcampian-Leonardian boundary is not paleontologically dated. Regional correlation suggests that the Wolfcampian-Leonardian boundary is near the Ingleside-Satanka contact. North of Owl Canyon the Ingleside intertongues with the Fountain and near the Colorado-Wyoming boundary, the Ingleside includes sediments of Atokan through Wolfcampian age (Hoyt, 1960).

TEXT-FIG. 1—*Triticites ventricosus* (Meek and Hayden) ×12, from Ingleside formation, Owl Canyon, Colorado.

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# ANOTHER NOMENCLATORIAL REVIEW OF THE CARBONIFEROUS LAMELLIBRANCHS *MACRODON*, *GRAMMATODON*, *PARALLELODON* AND *BEUSHAUSENIA*

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It has come to the writer's attention that the names of one genus of whales, two genera of fish, one carnivore, and five genera or subgenera of lamellibranchs have become somewhat confused. This perhaps is due to the obscure nature of the publications in which certain of these genera were discussed. Although a number of reviews and partial reviews of this subject have appeared in the literature, misuse of these generic names continues. For this reason, and because the validity of the subgenus *Cosmetodon* is questionable, a further discussion of the subject seems appropriate. Text-figure 1 illustrates the chronologic development of the nomenclature.

Illiger (1811, p. 142) used the generic name *Ancylodon* to designate certain ziphoid cetaceans possessing two obscure curved teeth in the upper jaw.

*Ancylodon*, though preoccupied, was used for certain sciaenid fishes by Bosc (1816, p. 497) in *Nouveau Dictionnaire d'Histoire Naturelle, etc.*, a work which was edited by Cuvier. Bosc apparently believed *Ancylodon* to be Cuvier's genus despite the fact that *Ancylodon* Illiger is discussed by Desmarest on the same page of the *Nouveau Dictionnaire*. Cuvier's first reference to *Ancylodon* as a sciaenid fish (1817, p. 299) did not appear until a year after the *Nouveau Dictionnaire* was published. *Ancylodon* of Bosc (1816, p. 497) and Cuvier (1817, p. 299) is invalid, the name being preoccupied by *Ancylodon* Illiger (1811, p. 142).

H. R. Schinz (1822, p. 482) was aware of Illiger's use of the name *Ancylodon* and, in his translation of Cuvier's *Le Règne Animal*. . . , which appeared under the title *Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der Vergleichenden Anatomie*, he substituted *Macrodon* for Cuvier's *Ancylodon*. Schinz's authorship of the name *Macrodon* has not been widely recognized, and this has complicated synonymy in both ichthyology and invertebrate paleontology.

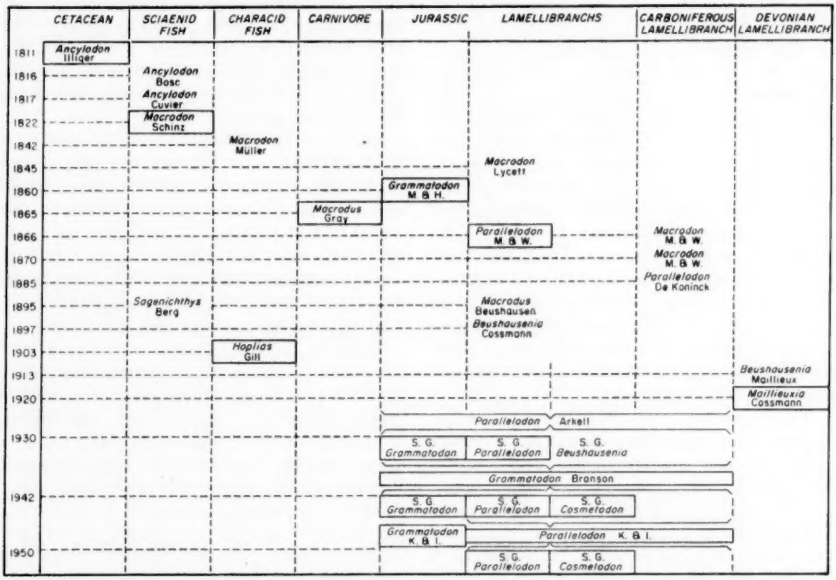
In 1895 (p. 52) Berg proposed the name *Sagenichthys* for the sciaenid fishes referred to *Ancylodon* by Cuvier. Jordan & Evermann (1895, p. 395) also adopted Berg's name *Sagenichthys*. This correction was not necessary, *Macrodon* having been proposed for this purpose by Schinz (1822, p. 482).

Gill (1903, p. 1015) has pointed out that Müller (1842, p. 308), not realizing that the name *Macrodon* was preoccupied, used *Macrodon* for a ". . . genus of the family of Erythrinids (by him associated with his family Characins)" (Gill, 1903, p. 1015). Gill (1903, p. 1015–1016) substituted *Hoplias* for *Macrodon* of Müller.

Lycett (p. 98), in Strickland & Buckman's revised 1845 edition of Murchison's *Outline of the Geology of the Neighbourhood of Cheltenham*, is credited with the name *Macrodon* as applied to certain fossil Jurassic lamellibranchs. Lycett apparently did not realize that the name was preoccupied.

Meek & Worthen (1866, p. 17), in a study of certain Carboniferous, arciform lamellibranch shells which they consider to belong to the genus *Macrodon* as defined by Lycett, recognized that *Macrodon* was preoccupied and invalid, stating, "Should it be thought desirable to change the name of this extinct genus, in consequence of the fact that Müller had used it for a genus of Fishes, in 1842, it might be called *Palallelodon*, from its elongate, parallel, posterior teeth." It is clear that *Parallelodon* was considered by Meek & Worthen as synonymous with *Macrodon* as defined by Lycett, and that since it is the first name proposed as a substitute for the preoccupied *Macrodon* Lycett, it must be preserved for that genus.

De Koninck (1885, p. 140–142) was the first worker to consider the Carboniferous arciform shells distinct from the Liassic shells referred by Lycett to *Macrodon*, an opinion not in agreement with that of Meek & Worthen. Although De Koninck realized that Meek & Worthen had proposed *Parallelodon* to replace *Macrodon* Lycett, he




TEXT-FIG. 1—Chronologic development of nomenclature. Generic and subgeneric names enclosed by dark lines are valid (see text discussion of validity of *Cosmetodon*); all other names are invalid. Note that Meek & Hayden are the authors of *Grammatodon* and that Meek & Worthen first proposed *Parallelodon*. Names of other workers following these names are intended only to facilitate reference to articles in which the limits of these genera were expanded or reduced. M. & H., Meek & Hayden; M. & W., Meek & Worthen; K. & I., Kobayashi & Ichikawa.

adopted *Parallelodon* for his Carboniferous arciform shells. A number of British workers (e.g., Hind, 1897, p. 125–130), although considering the Carboniferous and Jurassic arciform lamellibranchs to belong to different genera, followed De Koninck in the adoption of *Parallelodon* for the Carboniferous lamellibranchs. Hind (1897, p. 127) points out that American workers, including Meek & Worthen (1870, p. 40), have continued to use *Macrodon* for the Carboniferous arciform shells. Neither of these usages is satisfactory. *Parallelodon* Meek & Worthen should be adopted, as suggested by Meek & Worthen (1866, p. 17), as a replacement name for *Macrodon* Lycett, an invalid generic name for certain Liassic lamellibranchs. Cox (1929, p. 126) pointed out that this was the case and Arkell (1929, p. 37–38) used this name in reference to the genus called *Macrodon* by Lycett. *Macrodon*, as first defined by Schinz, must be retained for the genus of sciaenid fishes discussed by Bosc (1816, p. 497) and Cuvier (1817, p. 299).

In 1895 (p. 37) Beushausen, in the discussion of certain species which he considered congeneric with *Macrodon* Lycett, misspelled *Macrodon* as "*Macrodus*." As pointed out by Branson (1942, p. 247) some workers (Arkell, 1930, p. 303; Clark, 1907, p. 234) have erroneously believed that Beushausen was proposing a new generic name to replace *Macrodon*. This was not Beushausen's intention, and furthermore, the name *Macrodus* was used by Gray (1864, p. 536) for a genus of carnivore.

Cossmann (1897, p. 93), erroneously believing that the name *Parallelodon* should be applied to the Carboniferous arciform lamellibranchs as it was by De Koninck (1885, p. 140–142) and Hind (1897, p. 125–130), proposed the name *Beushausenia* be substituted for *Macrodon* Lycett. This correc-

tion was unnecessary because Meek & Worthen (1886, p. 17) had previously proposed *Parallelodon* for this purpose.

In 1913 (p. 33) Maillieux, unaware that the name had previously appeared in the literature, proposed to apply *Beushausenia* to a genus of Devonian lamellibranchs having affinities with *Pterinea* and *Leioptera*. Cossmann (1920, p. 137) pointed out that *Beushausenia* was preoccupied and proposed that the name *Maillieuxia* should be substituted for *Beushausenia* Maillieux. Despite the fact that *Beushausenia* Cossmann is a *nomen nudum*, Cossmann is correct in pointing out that the name is preoccupied and unavailable. It is apparent that *Maillieuxia* Cossmann is a valid substitution for *Beushausenia* Maillieux.

The arciform Carboniferous lamellibranchs discussed by Meek & Worthen (1866, p. 17) as *Macrodon*, and by De Koninck (1885, p. 140–142), Fischer (1887, p. 976), and Hind (1897, p. 125–130) as *Parallelodon* must, it would seem, receive a new name, *Macrodon* and *Parallelodon* both being preoccupied.

However, Arkell (1930, p. 297–306) included both Carboniferous and Jurassic Parallelodons, *Grammatodon* Meek & Hayden (1860), and *Beushausenia* Cossmann (1897) in a single genus, which he called *Parallelodon*. Branson (1942, p. 247–249) agreed with the grouping of these genera under one name but pointed out that the name, due to priority, must be *Grammatodon*. Branson also showed that *Beushausenia* Cossmann was nothing more than a substitute for *Macrodon* Lycett, hence, having the same type species, *Macrodon rugosus* Buckman. Arkell, not realizing this fact, had applied the name *Beushausenia* to a subgenus with *Cucullaea hirsonensis* d'Archaic as type. *Cucullaea hirsonensis* d'Archaic has no standing as the type of *Beushausenia* (= *Parallelodon*).

The title of Branson's article is *Parallelodon, Grammatodon, and Beushausenia* (= *Cosmetodon, new name*). Branson (p. 248) says "Arkell places the three subgenera *Parallelodon, Grammatodon*, and *Beushausenia* (= *Cosmetodon*) under the generic name *Parallelodon*." It is clear, from both the title and the quotation, that Branson is proposing *Cosmetodon* as a replacement name for *Beushausenia*. Branson proposes *Beushausenia keyserlingi* (d'Orbigny) as the type species of *Cosmetodon*. Unfortunately, if *Cosmetodon* equals *Beushausenia*, it necessarily has the same type species, *Macrodon rugosus* Buckman.

On the other hand, Branson (p. 248) just as clearly indicates that he is not proposing a replacement name stating "In order to avoid even the semblance of a replacement name and to fix the name (*Cosmetodon*) to available and well-illustrated specimens *Beushausenia keyserlingi* (Orbigny), 1850, illustrated by Arkell from Borissjack (Arkell, 1930, pl. 14, fig. 9,9a,10) is designated genotype."

There is little doubt that Branson understood the nomenclatorial problem involved and did not intend to submit a replacement name. However, if pagination is accepted as a valid guide in this problem, his title indicates that *Beushausenia* and *Cosmetodon* are equivalent. It is the writer's opinion that, because Branson's intention is fairly obvious, and because *Cosmetodon* is the first name which is not preoccupied to be proposed for this group of shells, it should be accepted as valid. It would appear that a final decision on this problem should be referred to the International Commission on Zoological Nomenclature.

As stated above, *Parallelodon, Beushausenia* as defined by Arkell (1930) (= *Cosmetodon*), and *Grammatodon* were grouped as a single genus by Arkell (1930) and Branson (1942). Subsequently, Kobayashi & Ichikawa (1950, p. 238) considered *Grammatodon* Meek & Hayden as a distinct genus and Nicol (1954, p. 96) not only considered *Grammatodon* as a distinct genus but placed it in the Cucullaeidae rather than the Parallelodontidae. By removal of *Grammatodon*, Mesozoic and Upper Paleozoic Parallelodons are confined to a single genus, *Parallelodon* (type species *Macrodon rugosus* Buckman), consisting of subgenus *Parallelodon* and the questionable, but probably valid, subgenus *Cosmetodon*, type species *Beushausenia keyserlingi* (d'Orbigny). In the future, should Carboniferous Parallelodons be considered as generically distinct from those of the Jurassic, a new name will be required for the former, inasmuch as no valid name now exists.

Because of the chaotic literature dealing

with these groups of lamellibranchs errors are easily compounded. For example, *Macrodon* was used in reference to a lamellibranch as late as 1941 (Saurin, p. 8) and *Macrodus* was so applied in 1942 (Spriesterbach, p. 175). It is hoped that text-figure 1, diagramatically illustrating the development of the nomenclature, may act to stabilize and lend uniformity to the use of many of these generic names.

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## A NOTE ON THE FISH FAUNA ASSOCIATED WITH THE PHYLLOCARID *MONTECARIS LEHMANNI* JUX IN THE DEVONIAN STRATA OF BERGISCH GLADBACH, WESTERN GERMANY

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In a recent issue of the JOURNAL OF PALEONTOLOGY (v. 34, no. 6, 1960), Dr. U. Jux has described a new phyllocarid crustacean, *Montecaris lehmanni*, from the upper "Plattenkalk" of the Bergisch Gladbach-Paffrath trough in the vicinity of Cologne, Western Germany, and in this connection also given certain comments on the accompanying fossils, invertebrate as well as vertebrate. The following note has been written with the intention of in some respects supplementing Dr. Jux' statements as regards the fish fauna of the deposits in question.

The list of fishes from the upper "Plattenkalk" on p. 1132 of the paper by Jux is based on preliminary determinations, made by the present writer in the fall of 1959, and not in that form intended for publication. When, shortly afterwards, the material had been subjected to detailed study, these determinations had to be altered in some respects (see further my account of the "Plattenkalk" fishes in Paläontologische Zeitschrift, v. 34, nos. 3–4, 1960; v. 35, nos. 1–2, 1961). The ptyctodontid Arthrodire first referred to as *Chelyophorus?* sp. turned out to belong to a new form, described under the name of *Ctenurella gladbachensis* ØRVIG; the Arthrodires also include a *Coccosteus?* sp.; the Crossopterygians comprise *Gyroptychius* sp. and *Thursius?* sp., whereas the presence of the genera *Glyptolepis* and *Diplocercides* of this particular group of fishes could not be corroborated with certainty; of Ganoids there are, in addition to *Moythomasia nitida* GROSS, also a *Stegotrachelus?* sp.; and among the Dipnoans, finally, one form has been described as *Dipterus* cf. *valenciennesi* SEDGWICK & MURCHISON and another as a new species of *Rhinodipterus*, *R. ulrichi* ØRVIG.

Speaking of the environmental conditions of *Montecaris*, Jux (*op. cit.*, p. 1142) stresses the purely marine (bathyal) facies of the upper "Plattenkalk" and mentions the possibility that the specimens of this crustacean "could have drifted in from a different living space, perhaps even from a continental area." "This idea," he goes on, "is not based only on the psilophyte remains but it finds a special support in the fish relicts" since, among them "there appear specimens that are characteristic in the Old Red and therefore completely unexpected in these . . . limestones." It is true enough that the fish fauna of the "Plattenkalk" is similar in many ways to that of e.g. the Scottish Middle Old Red Sandstone, and includes representatives of genera elsewhere known only from typical non-marine strata. Of the "Plattenkalk" fishes there are, on the other hand, a great many articulated specimens in such an excellent state of preservation that they cannot possibly have been transported very far post-mortem. Everything goes, in fact, to prove that in contradistinction to their relatives in the Middle Old Red Sandstone, the particular fishes with which one is here concerned originally had a marine habitat. In my opinion, this very possibly applies to *Montecaris* as well.

## *SYSTEMATOPHORA* KLEMENT AND *POLYSTEPHANOSPHAERA* SARJEANT

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During studies of microplankton assemblages from the Oxford clay (Lower Oxfordian) of Yorkshire, a species of hystrichosphere was encountered having a spherical shell bearing slender processes arising from the margins of circular areas of the shell

surface. These processes are linked together at their tips by a trabecula arising from the bifurcation of one process and meeting at right-angles the tips of the others of the group, thus forming a connecting ring. At the time, no similar forms had been described: a species from the Oligocene of Australia, with appendages originally described as "perforated tubes" (Cookson 1953) and subsequently as possibly grouped processes linked together at base and tip (Deflandre and Cookson 1955), had been described and placed in the genus *Cannosphaeropsis* O. Wetzel 1933 as *C. urnaformis*. O. Wetzel's genus comprises hystrichospheres with processes linked by trabeculae: following Cookson's precedent, this genus was used also to accommodate the Jurassic forms, which were named *C. calathus*.

Subsequent study of Dorset Upper Jurassic assemblages resulted in the discovery of two further species having processes grouped in circles. Of these, one from the Middle Callovian possesses processes comparable to those of *C. calathus*, but bending outward from their bases, in such fashion that each process cluster has a bell-shaped form, and widening at junction with the ring trabecula. Adjacent clusters are sometimes connected by trabeculae; these connecting trabeculae have, hanging from them at about mid-point, a membraneous filament. The second species, from the Upper Oxfordian, has processes of very varied form, simple, bifurcate, or ramifying, broad or slender, sometimes linked to adjacent processes in the same group either by basal coalescence or by cross-trabeculae at some point along their length (but never at their tip).

The discovery of these two further species rendered necessary the erection of a new genus to accommodate all three. The name *Polystephanosphaera* was proposed, with the Upper Oxfordian species, named *P. valensii* in honour of the French micropaleontologist L. Valensi (who described comparable hystrichospheres from undated French Upper Jurassic cherts), as type. The Callovian species was named *P. paracalathus;* and *C. urnaformis* was transferred to the new genus. In the paper proposing the new genus, which was expected to postdate in publication that written earlier, *C. calathus* is figured and is transferred to *Polystephanosphaera;* however it was subsequently realized that the papers would appear in reverse order and the generic attribution of this species was corrected in the first. The species was thus never published as *Cannosphaeropsis calathus* but only as *P. calathus*.

Although all four species were thus grouped into one genus on their possession of processes arranged in circles, it was realised that there were two distinct morphological groups, with the type species separated by lack of ring trabeculae.

Subsequent to publication of *Polystephanosphaera*, it was discovered that the German micropaleontologist K. W. Klement, in course of a full and scholarly work on the lower Malm (Upper Oxfordian-Lower Kimmeridgian) of Southwest Germany, had erected a new genus *Systematophora*, comprising hystrichospheres with processes arranged around circular or polygonal fields on the shell surface, the processes of each group simple, branching or ramifying, adjacent processes being sometimes linked by cross trabeculae. Three new species were placed within this genus. The type species, *S. areolata*, from Lower Kimmeridgian horizons, has an ovoid shell with a reticulate membrane, fourteen groups of processes regularly arranged and a girdle region of six elongate fields, each with a process at either end, in median position. The process groups are widely spaced so that their distribution is readily determinable; the processes are simple or with knobbed or branching tips. A second species, *S. fasciculigera* from Upper Oxfordian horizons, is of comparable general structure but has more numerous appendages, with abundant cross-connections in almost mesh-like fashion, in each group; the appendages ramify at their tips. The third species, *S. orbifera*, also of Upper Oxfordian age, is of roughly spherical shape and displays a similar number and arrangement of process clusters. The processes of each cluster are usually slender but occasionally quite thick; they are separate and without branches for much of their length, but branch distally, apparently in irregular fashion, adjacent branches coalescing so that each process is linked to its two neighbors.

The type species of *Polystephanosphaera*,

*P. valensii*, falls clearly within Klement's genus and, since publication of Klement's genus preceded that of my own by one month, *Polystephanosphaera* is a junior homonym of *Systematophora*. *S. valensii* nonetheless falls outside any of Klement's species, having a spherical shell with a granular, not reticulate, surface and with process clusters not certainly corresponding in distribution to the specified pattern; processes of extremely variable thickness and degree of ramification within each cluster; and frequent linkage of adjacent processes by cross trabeculae at points along their length but never at their tips. Although clear morphological comparisons exist with the other species of the genus, no obvious evolutionary pattern suggests itself.

The three remaining species attributed to *Polystephanosphaera* fall clearly outside Klement's genus; a new genus is therefore here proposed to accommodate them:

Order HYSTRICHOSPHAERIDIA
Family HYSTRICHOSPHAERIDAE
Genus POLYSTEPHANEPHORUS, n. gen.

*Type species.*—*Polystephanephorus calathus* (Sarjeant 1961)

*Diagnosis.*—Hystrichospheres bearing processes, solid or hollow and closed distally, whose points of origin are arranged in circles or polygons, the groups of processes thus formed being arranged in a set pattern or at constant intervals over the shell surface. The processes of each group are connected together at their tips by a trabecula in the form of a ring, typically formed by the bifurcation of one process and the extension of its branches, parallel to the shell surface, to meet at right-angles the tips of the other processes of the group; each cluster thus has the appearance of an open-walled and open-ended tube. Individual processes may show linkage to adjacent processes by basal extension or by development of connecting trabeculae at positions along their length.

*Remarks.*—The special character of the hystrichospheres of this genus is the possession of clusters of processes linked at their tips by ring-trabeculae. The species *P. paracalathus* (Sarjeant 1960) and *P. urnaformis* (Cookson 1953) share this character and are assigned to this genus.

*Acknowledgments.*—The valuable assistance in discussion of Mr. T. G. Miller and Dr. T. P. Burnaby, of Keele, and in correspondence of Mr. A. G. Brighton, Curator of the Sedgwick Museum, Cambridge, is most gratefully acknowledged.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1097, SEPTEMBER, 1961

# NOTICES

## THE KARL P. SCHMIDT FUND

The Karl P. Schmidt Fund has modest sums available to assist persons wishing to study at the Chicago Natural History Museum. Grants will be made for study in any of the four fields encompassed by the museum: anthropology (with a natural history orientation), botany, geology (including paleontology), and zoology. An applicant should describe the study proposed in brief terms, state the length of time he wishes to study at the museum and the amount of money needed, and name one reference.

Applications should be mailed to: Chairman, The Karl P. Schmidt Fund, c/o Chicago Natural History Museum, Roosevelt Road and Lake Shore Drive, Chicago 5, Illinois.

## CATALOGUE OF TYPES

"Mississippian Plant Spores from the Hardinsburg Formation of Illinois and Kentucky"

By W. S. HOFFMEISTER, F. L. STAPLIN AND R. E. MALLOY

JOURNAL of PALEONTOLGY, v. 29, no. 3, May 1955, pp. 373–399

See pp. 373, 377 and 380 for keys to localities and stratigraphic occurrences

| | | |
|---|---|---|
| *U.S.N.M.* | 41313 | *Acanthotriletes echinatus*, holotype |
| | 41314 | *A. echinatus*, paratype |
| | 41315 | *Apiculatisporites pineatus*, holotype |
| | 41316 | *Auroraspora solisortus*, genotype |
| | 41317 | *Cirratriradites granulatipunctatus*, holotype |
| | 41318 | *C. praetergranulatus*, holotype |
| | 41319 | *C. pseudoanulatus*, n. comb. |
| | 41320 | *C. uber*, holotype |
| | 41321 | *Calamosphora* type A |
| | 41322 | *Convolutispora ampla*, holotype |
| | 41323 | *C. florida*, genotype |
| | 41324 | *C. florida*, paratype |
| | 41325 | *C. mellita*, holotype |
| | 41326 | *C. tessellata*, holotype |
| | 41327 | *C. venusta*, holotype |
| | 41328 | *Densosporites brevispinosus*, holotype |
| | 41329 | *D. capistratus*, holotype |
| | 41330 | *D. parvus*, holotype |
| | 41331 | *D. spinifer*, holotype |
| | 41332 | *D. tenuis*, holotype |
| | 41333 | *D. tenuis*, paratype |
| | 41334 | *D. tenuis*, paratype |
| | 41335 | *D.* type A |
| | 41336 | *Endosporites minutus* |
| | 41337 | *Endosporites* type A, hypotype |
| | 41338 | *E. endorugosus*, holotype |
| | 41339 | *Grandispora spinosa*, genotype |
| | 41340 | *G. spinosa*, paratype |
| | 41341 | *Granulatisporites tuberculatus*, holotype |
| | 41342 | *G. politus*, holotype |
| | 41343 | *Knoxisporites rotatus*, holotype |
| | 41344 | *K. triradiatus*, holotype |
| | 41345 | *K. triradiatus*, paratype |
| | 41346 | *Microreticulatisporites fundatus*, holotype |
| | 41347 | *Punctatisporites? baccatus*, holotype |
| | 41348 | *P. fissus*, holotype |
| | 41349 | *P. grandis*, holotype |
| | 41350 | *P. nitidus*, holotype |
| | 41351 | *P. plicatus*, holotype |
| | 41352 | *P. reticulopunctatus*, holotype |
| | 41353 | *P.? cerrosus*, holotype |
| | 41354 | *P. callosus*, holotype |
| | 41355 | *P. pseudolevatus*, holotype |
| | 41356 | *P.?* type A, hypotype |
| | 41357 | *P.* type B, hypotype |
| | 41358 | *P.* type C, hypotype |
| | 41359 | *Raistrickia multipertica*, holotype |
| | 41360 | *Reticulatisporites decoratus*, holotype |
| | 41361 | *R.* type A, hypotype |
| | 41362 | *R.* type B, hypotype |
| | 41363 | *Schultzospora elongata*, holotype |
| | 41364 | *Triquitrites marginatus*, holotype |
| | 41365 | *T.* type A, hypotype |
| | 41366 | Spore type A, hypotype |
| | 41367 | Spore type B, hypotype |
| | 41368 | Spore type C, hypotype |
| | 41369 | Spore type D, typotype |

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# REVIEW

OLIGOCENE PLANTS FROM THE UPPER RUBY RIVER BASIN, SOUTHWESTERN MONTANA. Herman F. Becker. Geological Society of America Memoir 82. vii + 127 p., Illus. 1961. $3.00 (Fellows and Members of G.S.A.), $4.25 (non-members).

A considerable amount of information concerning Oligocene vegetation in western North America has come from study of the numerous and well-preserved plants in the Florissant beds of Colorado. Additional data is provided by Dr. Becker's study of the Ruby flora in southwestern Montana. The flora consists of 37 families, 61 genera, and 82 species (60 of which are extant). Twenty-five new species are described. The most abundant elements in the flora are *Metasequoia, Pinus, Abies, Picea, Zelkova, Alnus, Cercidiphyllum, Ailanthus,* and *Fraxinus.* Living equivalents of the fossil species are distributed in the eastern United States, western United States, and eastern Asia.

Several plant communities and habitat conditions are suggested by the flora: Hydrosere (*Cyperacites, Potamogeton, Typha*), Floodplain and Humid-Forest Community (*Alnus, Cercidiphyllum, Dennstaedtia, Glyptostrobus, Holmskioldia, Metasequoia, Myrica, Osmunda*), Riparian Association (*Acer, Celtis, Cornus, Fraxinus, Nyssa, Populus, Ptelea, Salix, Smilax, Zelkova*), Deciduous Forest (*Acer, Betula, Carpinus, Fagus, Quercus, Ulmus*), Coniferous Forest (*Abies, Chamaecyparis, Picea, Pinus, Pseudotsuga*) and a Xeric association (*Cardiospermum, Cerocarpus, Cotinus, Mahonia, Paliurus, Philadelphus, Potentilla, Quercus, Ribes,* and *Sapindus*).

The age of the flora is considered to be late Oligocene. This conclusion is based on the similarity between it and the Florissant flora. Approximately 40% of the Ruby species overlap with the Florissant flora. *Cotinus fraterna, Fagopsis longifolia, Populus crassa, Mahonia obliqua,* and *Philadelphus parvulus* are species known only from the Ruby and Florissant floras and serve as the principal floristic basis for age determination.

The results of the study are presented in a logical and well-organized sequence. Topic headings include Life Zones and Modern Vegetation of the Ruby Region, Physical and Geological Aspects of the Ruby Region, Fossil Localities, Composition of the Tertiary Ruby Flora, Ecological Aspects of the Fossil-Shale Zone, Age of the Flora, Conclusions and Summary, Systematics (Methods of identification, Systematic descriptions, Corrections of names). The photographs are adequate, although some lack sufficient detail for specimen comparison (*i.e.*, pl. 7, fig. 14; pl. 14, fig. 9). The publication contains a bibliography of 97 references.

One minor criticism of the document is Dr. Becker's designation of holotypes. The fish and insect remains and several plant fossils (cf. pl. 11, figs. 13–23) are listed as holotypes, without description or species designation. In biological practice a holotype is the specimen upon which a species description is based; consequently, there can be none for a species which has not been described. In a few instances (*i.e.*, pl. 7, figs. 12,13,17–19) more than one specimen is designated as holotype, whereas there can be only one. This misuse of the term is puzzling since the author defines a holotype as "a single specimen upon which a new species is based" (p. 43). This, however, does not seriously affect the significance of the study. Assuming identifications to be correct, his data appears well interpreted and his conclusions sufficiently documented. The study represents a substantial contribution to our knowledge of Oligocene vegetation.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 1099–1102, SEPTEMBER, 1961

# SOCIETY RECORDS AND ACTIVITIES

## BALLOT OF THE MEMBERSHIP REGARDING INCREASE OF DUES

To the Council of the Paleontological Society:

We, the undersigned, have examined the ballots returned to the Secretary's office by May 15 in the vote on the increase of dues for the Paleontological Society and find the following results:

1. Total number of ballots returned—294.
2. The vote was as follows:

| | |
|---|---|
| For | 259 |
| Against | 33 |
| Blank | 2 |

Respectfully submitted,
(Signed) ALLEN R. ORMISTON
FRED C. SHAW
ZEDDID P. BOWEN

MCZ, Harvard University
Cambridge 38, Mass.
18 May 1961

## PROPOSED NEW MEMBERS

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the names of new members approved by the council are as follows:

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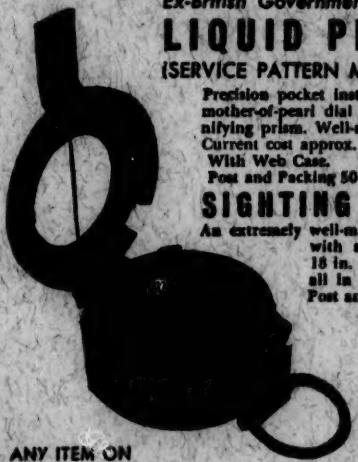

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